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JOURNAL OF ANATOMY

# THE FUNCTION OF THE EPIGLOTTIS

By V. E. NEGUS, M.S., F.R.C.S.
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## PREVIOUS VIEWS OF FUNCTION

It was at one time thought that the epiglottis acted as "the lid of the larynx"; it was supposed that during deglutition it fell back like a flap over the laryngeal aperture in order to prevent ingress of food or water. This erroneous view was dispelled by Stuart, who proved that during swallowing the epiglottis actually moved forwards, to be squeezed between the base of the tongue and the rest of the larynx. This view cannot be disputed by anyone capable of judging, and the truth of it is borne out when observing a patient whose epiglottis has been almost entirely destroyed by lupus, but whose powers of swallowing remain unaffected.

Having disposed of the prevailing theory as to the function of the organ Stuart did not supply any alternative; therefore the subject can be approached without any bias or preconceived ideas.

## LACK OF NECESSITY DURING DEGLUTITION

The greater part of the epiglottis can be dispensed with in Man without detriment to deglutition, and similar conclusions as to its lack of importance in regard to this function are derived from observation of many of the lower animals, in which no traces are found. Examples are seen in frogs, salamanders, newts, snakes, lizards, crocodiles, alligators, tortoises, turtles and Birds. It is true that there is a rudiment present in certain teguexin, monitor and iguana lizards, in some pythons and copper-head snakes, in boa constrictors, and in certain storks, herons and one or two other birds.

The remainder of the animals mentioned have no epiglottis and yet they swallow easily, while among Mammals, the sea lion also is found to be almost destitute of the organ.

## LACK OF NECESSITY DURING RESPIRATION

With regard to respiration there is no real necessity for the presence of an epiglottis. When a man runs fast he opens his mouth widely, and, on the authority of Prof. Leonard Hill, he gains thereby, as the cool air entering his lungs is an actual advantage to him. In Birds, lizards, and many other animals, air enters by the mouth during exertion with no detrimental effects, and for this and for other reasons it is concluded that the epiglottis was not



E.B. 1-18-29

Fig. 1. View from above of larynx of alligator (*Crocodilus americanus*) (left), J 225. 4. R.C.S. Museum (natural size); spotted hyaena (*Crocuta maculata*) (right) (natural size). In the former there is no epiglottis and in the latter the organ does not prevent inundation of the posterior end of the laryngeal aperture; therefore the aperture must be closed in both animals during the swallowing of liquids.

Fig. 2. Sagittal section of head of a penguin (*Spheniscus demersus*). ($\frac{3}{4}$ natural size.) The absence of an epiglottis allows all air to enter by the mouth when the latter is open.

developed for respiratory purposes, although—as will be pointed out later—it does, in certain instances, add to efficiency in this respect.

## LACK OF NECESSITY DURING PHONATION

The function of phonation again does not require an epiglottis; in man the organ does not appear to assist in phonation, and in song birds there is no epiglottis at all; gibbons are poorly provided for and sea lions have nothing more than a rudiment.

Consequently some other reason must be looked for.

## OLFACTORY FUNCTION OF EPIGLOTTIS

It is found that the epiglottis is best developed in such animals as deer and antelopes, and on examining all species it is borne in on the observer that it is in the macrosmatic animals that development is best, while in microsmatic species it is deficient.

The correct route by which to arrive at any conclusion is to compare the anatomical structure of each animal with its habits; the result of such a study need not be set out in detail, as it will suffice merely to mention what deductions have been made.

In brief it is concluded as the result of observation that the epiglottis is an accessory olfactory organ, and that its primary function is to aid certain species which rely on powers of scent, sometimes for their actual existence.

An antelope or deer has to spend a large amount of time in grazing, as it must consume a great deal of grass in order to derive sufficient nourishment. It eats with its tail to the wind so that the scent of any enemy may be borne down wind to it; at the same time the laterally placed eyes keep watch on either side and in front. By this means it is protected on all four sides against sudden attack, but when its eyes are engaged in keeping watch it is impossible for them to see what is being eaten. Therefore the animal has its anterior nostrils placed in close proximity to its mouth in order that the odour of all prospective food shall reach the olfactory nerve endings and be appraised before any mouthful is swallowed.

While the animal is cropping grass or other herbage its tongue assists in drawing grass, leaves, or shoots towards the teeth and the mouth itself is partly opened. Under such conditions the natural tendency would be for the greater part of the inspired air to enter by the mouth and not by the more narrow nose. But if the olfactory sense is to be keen enough to detect both enemies and poisonous food-stuff it is a necessity that a large current of air should enter by the nose to pass over the olfactory mucous membrane. It is found that the means of attaining this end and of preventing the mouth from admitting air is by the provision of an epiglottis. The organ effectively shuts off the buccal cavity and ensures that all inspired air shall enter by the nose.

Animals without this arrangement—such as Birds, snakes, tortoises, or sea lions—cannot be keen scented when the mouth is open, while others such as

Fig. 3. Saggital section of head of a muntjac or barking deer (*Cervulus muntjac*), showing how the epiglottis shuts off the mouth from the air stream. (⅔ natural size.)

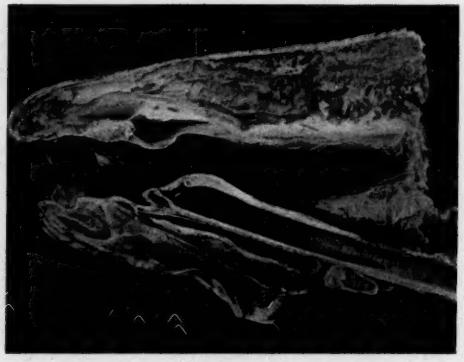

Fig. 4. Sagittal section of head of a python (*Python molurus*) in which the olfactory sense must be feeble when the mouth is open. (⅔ natural size.)

deer, antelopes, wolves, and lions are able to open the mouth widely and yet to preserve undiminished the integrity of their powers of scent.

The corollary is that most of those animals with a degenerate or without any epiglottis are microsmatic, while those with an efficient organ are for the most part keen scented.

Aquatic animals like sea lions and keen-sighted species like man, are microsmatic and do not need an efficient epiglottis; a few species deficient in powers of scent are found to retain a big one for other reasons.

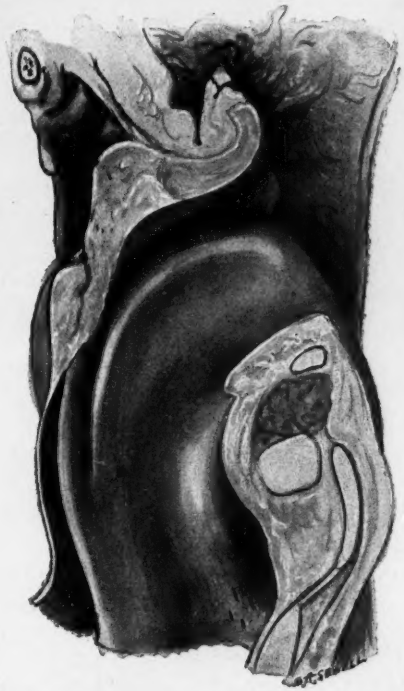

Fig. 5. Right half of larynx of a Californian sea lion (*Otaria gillespii*) in which the epiglottis is extremely degenerate. (1172 Lea. R.C.S. Museum.) (Almost natural size.)

## ASSOCIATED DEVELOPMENT OF SOFT PALATE

To enable the epiglottis to shut off the mouth it is necessary that the nasal air tube should be long if the air tract is to be complete from the anterior nostrils to the trachea. This end is attained by lengthening of the soft palate in order that the epiglottis may lie above it in the intra-narial position and thus bring the laryngeal aperture into direct communication with the nasopharynx.

Lateral palatine folds are also necessary to complete the partition at the

hinder end of the mouth; these folds are approximated to the lateral folds of the epiglottis, or to the side of the ary-epiglottic folds in certain instances.

In microsmatic man the soft palate is relatively short and does not reach the epiglottis.

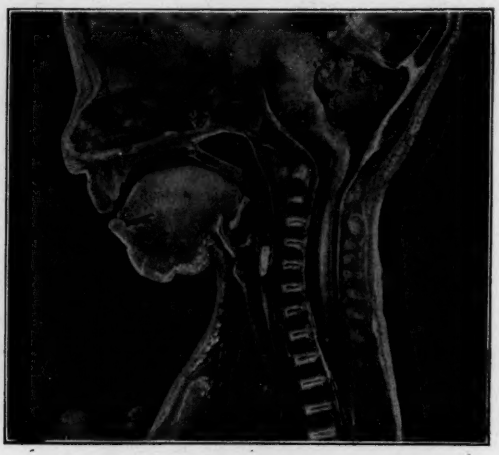

Fig 6. Right half of the head of a human foetus at the seventh month. The epiglottis is relatively small and the soft palate is short; there is no means of preventing entrance of air by the mouth when it is open except by approximation of the tongue against the palate. ($\frac{1}{2}$ natural size.)

## SECONDARY FUNCTION IN RESPIRATION

In fast-running keen-scented animals the big epiglottis is tilted downwards together with the aperture of the larynx in such a way that the air tract is almost straight and devoid of eddies, whereby passage of air in and out of the lungs is facilitated.

## SECONDARY FUNCTION IN DEGLUTITION

Lateral epiglottic folds are useful in preventing inundation of the anterior end of the larynx, and ary-epiglottic folds are still more efficient.

In the latter instances however the part of the epiglottis above the level of the ary-epiglottic folds is of no importance in deglutition, as may be seen in men in whom disease has left merely the ary-epiglottic folds after destroying the greater part of the epiglottis itself.

In herbage-eating species and particularly in Ruminants the larynx is high and spout-like and is surrounded by a muscular sphincter or arcus palato-pharyngeus made up of very long lateral palatine folds which meet behind the laryngeal aperture. In whales and dolphins this arrangement is extremely well marked and is highly efficient in allowing respiration to continue while the mouth and pharynx are full of water.

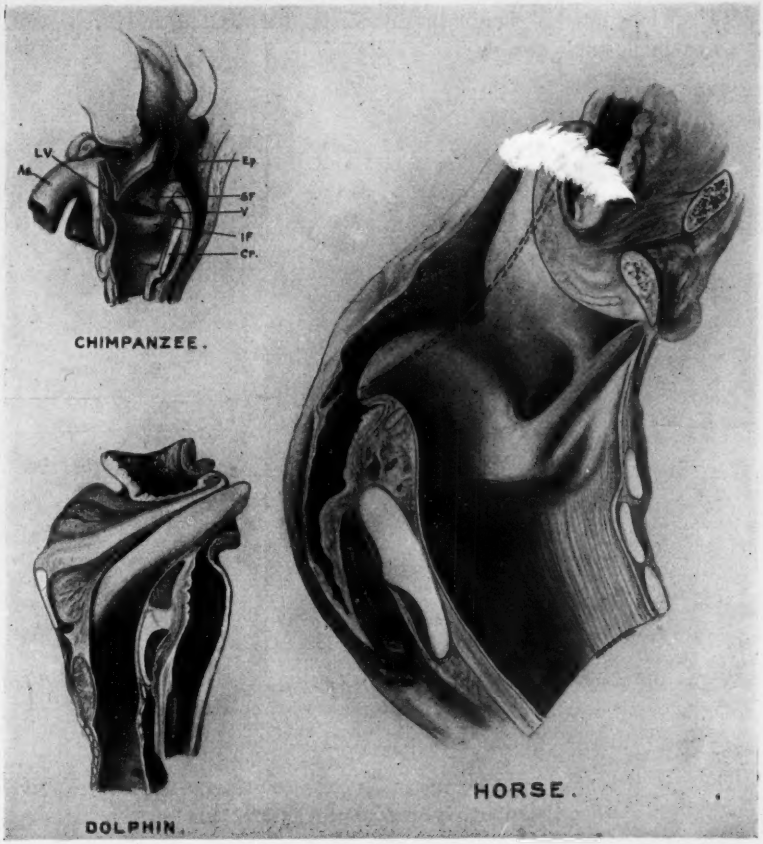


Fig. 7. Section of larynx to show the secondary function of the epiglottis in helping to form a spout through which air may enter, while food or water pass along channels on either side. In the chimpanzee (*Anthropopithecus troglodytes*) the mechanism does not exist. Horse *Equus caballus*) and dolphin (*Delphinus delphis*) show it well.

## FUNCTION OF HYO-GLOSSO-EPIGLOTTIC MUSCLE

When a big epiglottis is present it must be held forward during respiration to press against the upper surface of the soft palate, thus keeping the air way freely patent. When the swallowing of a big bolus takes place the epiglottis leaves the soft palate and takes up a position at the base of the tongue.

The mechanism by which it is pulled forward in both cases is provided by the hyo-glosso-epiglottic muscle, which is big and powerful in all animals whose epiglottis is big and mobile.

In man the organ is degenerate in function and is separated from the soft palate by a long interval; in him the muscle has disappeared, and is represented by a hyo-epiglottic ligament.

Fig. 8. Dissected larynx of a fox terrier dog (*Canis familiaris*). The hyo-glosso-epiglottic muscle is strong and the epiglottis is big and mobile. (Natural size.)

## SUMMARY

The epiglottis appears to be present in order to preserve the integrity of the olfactory sense when the mouth is open. It carries out this function by coaptation to a long soft palate, thereby preventing entrance of air by the mouth.

An epiglottis is not necessary for purposes of deglutition, respiration, or phonation; in certain animals, however, it serves a secondary function during the swallowing of liquids and semi-solids, and it can also be of assistance in respiration.

*Note.* Four of the illustrations have been published previously in the *Journal of Laryngology and Otology*, and the *Lancet*; acknowledgment is made with thanks to these journals for their reproduction here.

The drawings are by Mr S. A. Sewell and the photographs are by Mr Henry George.

Most of the specimens illustrated are in the possession of the author and were obtained through the courtesy of the Zoological Society of London; the remainder are in the Museum of the Royal College of Surgeons of England, and are reproduced by permission.

# THE DEVELOPMENT OF THE LOWER END OF THE VAGINA

By ALICE BLOOMFIELD, M.D., F.R.C.S. (*William Gibson Research Scholar*)

AND

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Although a considerable amount of work has been done on the development of the lower end of the vagina and its associated structures, such as the hymen, it is nevertheless true that uniformity of opinion on the subject has not been reached. Partly, no doubt, this is due to much of the research having been carried out on non-human material, the human processes being assumed to be parallel if not identical, a supposition which appears to contain many fallacies. Possibly, also, some of the suggestions put forward may have been advanced on insufficient grounds, such as scantiness of material, or want of careful examination by serial sections of the parts above and below the region concerned. Whatever may be the cause, it is evident that not only descriptive discrepancies in detail, but utterly opposed differences in fundamental origins are to be met with by any who are seeking guidance in this developmental field. Clinicians and pathologists have been suggesting for many years that, from their respective standpoints, there is reason to suppose that the lower end of the vagina and hymen may have a developmental value which differs from that of the vagina higher up, and it is no doubt owing to this clinical impression that so much work has been done on the matter. The results of this work may be shortly summed up for present purposes by saying that—disregarding differences in detail—three main views emerge—the vagina may be held to be purely Müllerian in its origin, or it may be mainly Müllerian, but with an additional (Wolffian) factor present and taking part in the formation of its lower part, or, lastly, it may be largely if not altogether a derivative of the urogenital sinus. We will consider these views more fully in the final part of this paper, it being enough at the moment to recall the apparently irreconcilable differences between them, and thus to have a conception of the main questions at issue.

As we were engaged on certain investigations concerned with the development of the female genital system, and were hindered to some extent by the evident want of reliable data on the formation of the lower part of the genital tract in women, we attempted to determine the matter conclusively for ourselves. The present paper gives our results in a condensed but, we hope, useful form. The research was carried out exclusively on human material, and by the method of examination of serial sections and by reconstructions.

There is little or no question about the parts played by the Müllerian and Wolffian ducts during the first three months of intra-uterine life. The Wolffian duct is present at a very early stage, and soon reaches and opens into the cloacal cavity. The Müllerian duct, appearing first at its proximal end at or before the 10 mm. stage, extends gradually distally in close relation with the Wolffian duct: it lies at first rather lateral and ventral to this last-named tube, but in the pelvis comes to lie to its inner side, in contact with its fellow. The two Müllerian ducts come into relation with each other in the pelvis about the stage of 28–30 mm., and then, following the curved course of the Wolffian ducts between which they lie, they extend toward the posterior wall of the urogenital sinus, which they reach at about 36–38 mm. The four ducts, grouped in this way, are surrounded by a mesodermal condensation, the so-called "genital stalk." The Müllerian ducts, within the

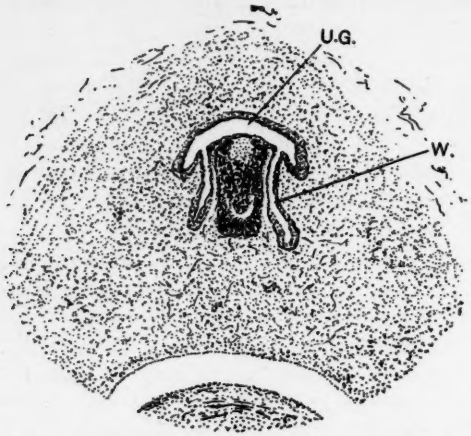


Fig. 1. Section through the terminal parts of the Wolffian and Müllerian ducts in an embryo of 38 mm. *U.G.*, urogenital sinus; *W.*, Wolffian duct. The double nature of the Müllerian terminations between the two Wolffian ducts is apparent. The surrounding condensation is the genital stalk.

"stalk," have well-marked lumina, and are in contact at first with one another. Their inner walls, however, quickly fuse and disappear, so that a simple tube appears in this part, the change seemingly taking place from above downwards, but not affecting so completely the terminal parts close to their attachment to the wall of the sinus.

Fig. 1 is from a section from an embryo of 38 mm. and shows the four ducts and the urogenital sinus. The two Wolffian ducts have clear but small openings into the sinus, while the Müllerian ducts appear at first to be represented by a mass of darkly-staining cells: closer examination of this mass, however, reveals the separate tracks of the two ducts, the thickened walls of which—fused where they are in contact—make the cellular mass.

An examination of the whole length of the utero-vaginal portion of the Müllerian structures in this embryo shows very clearly how the double tube forms a single median channel below the level of the future uterine cornua, but it can be seen that the fusion, or, more accurately, the disappearance of the basic double nature of the structure, does not take place at the lower end (which is shown in fig. 1) in contact with the wall of the sinus.

We have no desire at present to suggest any reason for the partial persistence of the paired condition at the lower end of this Müllerian structure, as just described, but we may point out here that the somewhat paired appearance (which we are about to describe) of the earlier bulbous growths at the lower end of the vagina may be due to their origin from this still double rudiment.

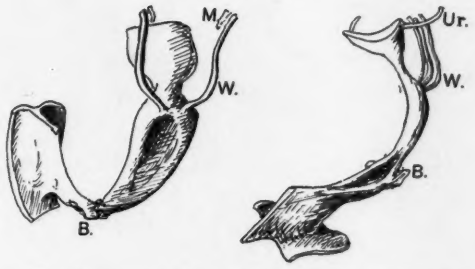


Fig. 2. Sketches from "cast" reconstructions, to show the general form of the urogenital sinus in 28 mm. and 38 mm. embryos. The younger specimen, seen from the left and behind, is shown at more than twice the magnification of the other, viewed from the left front. Upper and lower parts of the sinus (p. pelvina and p. phallica of Felix) are easily distinguished. *B.*, the rudiment of Bartholin's gland, is at the upper end of the lower part. This part has its roof depressed in a longitudinal "keel" (38 mm.) which later extends into the upper part: in this there is an impression on the floor (28 mm.) of uncertain meaning. *Ur.*, ureter; *W.*, Wolffian duct; *M.*, lower end of Müllerian duct, not yet reaching sinus.

Fig. 1 shows the dorsal projection into the cavity of the urogenital sinus, at the level of the ducts, which is termed the Müllerian tubercle. The sinus is really crescentic on section at this part, perhaps owing to the presence of the more solid condensation in relation with its posterior wall.

The sinus urogenitalis presents most interesting changes during development, and the history of this region deserves fuller consideration than it seems to have received. We are only concerned indirectly, however, with this part in the present paper and cannot enter into any long description of it. Its continuation above the level of attachment of the ducts leads, of course, to the bladder, and may be termed without prejudice the urethra. Below this level the sinus appears to consist of two parts: a "lower," opening on the surface and relatively wide, with a longitudinal and broad keel-like ridge along the roof, and an "upper" part, at first fairly long and with a narrower lumen. Bartholin's glands begin as solid outgrowths from the upper end of the lower part—about the stage of 30 mm., or perhaps before this. This spot,

marked in subsequent stages by the position of the junction of the gland duct with the sinus, is, from our present point of view, the important feature of the sinus. It can be taken as practically fixed in position and unaffected by subsequent longitudinal foldings or groove-formations in the wall of the sinus. Fig. 2, from a couple of "cast" reconstructions of the sinus in embryos of 28 mm. and 38 mm., will give an idea of the appearance of the region and the condition of the Bartholin rudiments at these stages.

Slow growth *in situ* now goes on. It is not necessary to describe these successive slow changes, and it will suffice to say that, by the time that the stage of 55 mm. is reached, certain alterations have occurred in the lower end of the utero-vaginal canal: the upper part of the canal has its lumen

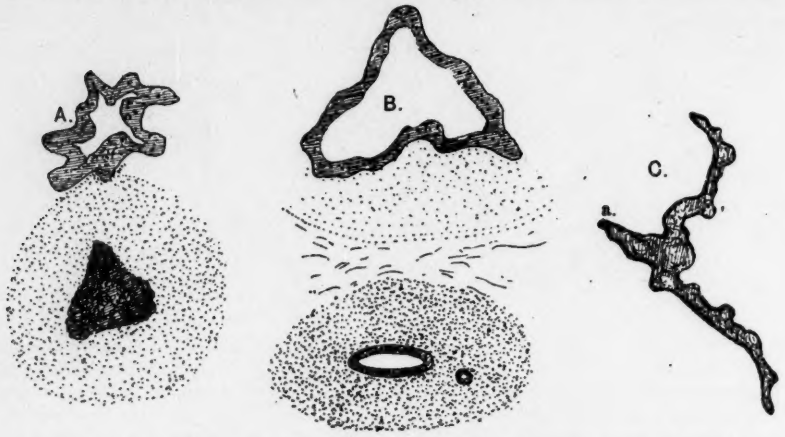


Fig. 3. A. and B., sections at different levels through the utero-vaginal canal of an embryo of 55 mm. In the higher section (B.) a Wolffian duct is seen. The lower section (B.) is a very little distance above the site of contact with the sinus. C., section through the canal in a specimen of 79 mm., above the region of main enlargement, to show the triradiate shape and the beginnings of distinct areas of cell proliferation.

lined by high columnar epithelium, and is surrounded by a definite mesodermal condensation distinct from that surrounding the bladder. As it is traced down towards the region where, in the 38 mm. specimen (fig. 1), the original two lumina were still distinguishable, we find that the single lumen becomes smaller, finally disappearing in a central solid plug of cells which lies between two somewhat rod-shaped lateral cell masses. These last evidently represent the double rudiments of the earlier state, now become altogether solid from proliferation of their lining cells. The central plug is apparently the direct derivative of the fused mesial walls of the two tubes, undergoing proliferation, and forms a ridge projecting forward and giving a form to the whole which is somewhat triangular or T-shaped on section.

Fig. 3 (*A.* and *B.*) shows sections through this region. The anterior process reaches the wall of the sinus further on, and extends a little way downwards

along it. Here it is to be noticed that the cellular mass has also broken into the sinus, as shown in fig. 4. This is an important fact, distinguishing this stage from that last figured, in which the vaginal and sinus epithelia came into contact and blended, but there was no true communication between the cavities: in the 55 mm. specimen there is an actual disruption of the sinus epithelium covering the site of contact, and therefore a true—though for the time being only a potential—communication is formed between the cavity of the sinus and the utero-vaginal canal, here represented by a solid epithelial mass.

The Wolffian duct can be traced for a few sections in this 55 mm. specimen as a patent tube lined with a sharply-cut epithelial layer, lying lateral to the

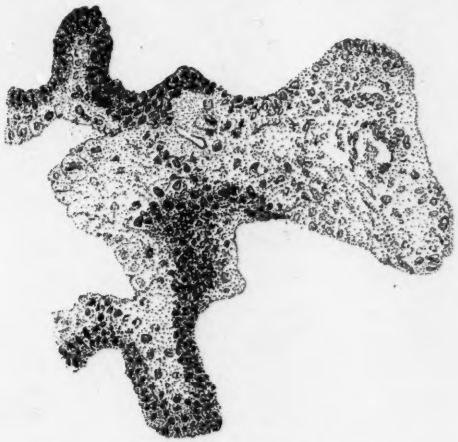

Fig. 4. Section showing vaginal epithelial mass (on right) breaking the epithelial lining of sinus (left), 55 mm.

utero-vaginal canal, perfectly distinct from it but situated within the condensation surrounding it. No trace of the Wolffian duct could be found on either side in the neighbourhood of the communication between sinus and vagina.

As exemplified in this specimen, we have found in later stages the presence and persistence of the Wolffian duct to be very variable. Very occasionally its lower end may persist in its entirety, at any rate on one side. More often it can be picked up in serial sections for a short distance and on one side only, to be lost further on, while occasionally at a lower level, it, or the duct of the other side, may be traced again for a little distance.

The sinus, still relatively long and narrow, has a well-marked groove on each side wall, into which the duct of Bartholin's gland opens. The gland itself is represented by a small mass of rudimentary alveoli lying in the mesoderm lateral to the sinus. The position of the opening of the duct, and

its relation to the site of contact of the vaginal structures is very much the same as before, about half-way up the sinus: this situation holds for some time, and the state of the parts at 55 mm. is practically the same as that seen in fig. 6.

A specimen of the 65 mm. stage may be mentioned here, not because any marked change has taken place in the parts, but because one Wolffian duct remnant can be traced in it in the neighbourhood of the greater part of the length of the utero-vaginal canal. It is first picked up (fig. 5) as a small distinct cord (? tube with very small lumen) lying laterally: traced down, it can be seen to enter the sinus just below and lateral to the junction between the latter and the utero-vaginal canal. The remnant is some little distance

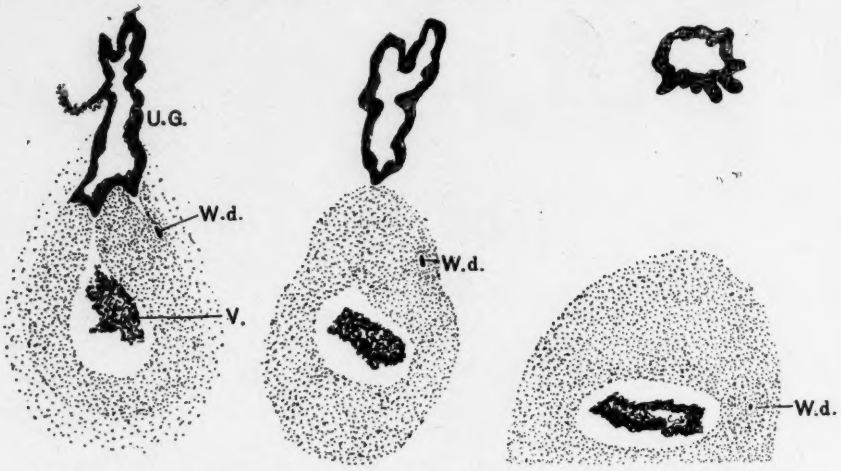


Fig. 5. Sections to show remnants of Wolffian duct on one side, 65 mm. *V.*, vaginal epithelium, shrunken; *U.G.*, urogenital sinus; *W.d.*, Wolffian duct.

from the Müllerian structures, although embedded in the surrounding condensation. It is evidently in an atrophic state, presumably about to disappear.

The central fact, at the stage reached so far, is the evidence of a certain amount of activity in the Müllerian derivatives at, and for a little distance above, their area of contact with the sinus. A stage a little later, one of 79 mm., shows the beginning of a further and definite evolution in this activity. In this specimen the epithelial proliferation at the lower part of the utero-vaginal canal has assumed certain definite characters, progressing mainly at three "centres" which, however, are naturally continuous. Of these two are laterally and the third centrally placed, so that three bulbous swellings, of irregular outlines, are produced: the lateral "bulbs" are somewhat larger than the central one, which projects more like a keel on the front surface, and makes the contact with the wall of the sinus. The cells forming these

bulbs assume a somewhat concentric arrangement, the innermost cells becoming large, rounded, and vacuolated, with a tendency to break down, the whole bulb giving the impression on section of a "cell-nest." Although there are three main "centres," it must be understood that there are many small and separate ones as well, and the area of this growth extends for a considerable distance up the vaginal canal.

The triradiate or T-shaped form of the vaginal mass, as seen on section and mentioned in earlier stages, is preserved in this, the definite bulbar formations being essentially only further elaborations of the former central and lateral thickenings (see fig. 3, *C.*).

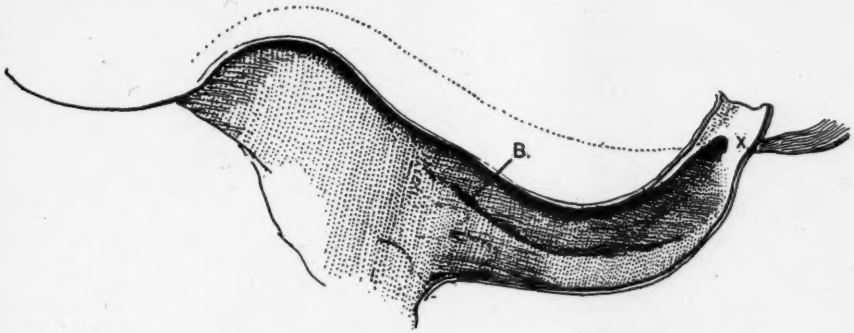


Fig. 6. Sagittal section of sinus of 65–70 mm. specimen. Reconstruction. *B.*, opening of duct of Bartholin's gland; *X.*, site of vaginal contact. The dotted line marks the level of the longitudinal sinus running beside the "keel" of the roof, which is cut along its length.

In this particular specimen there is an interesting condition to be noted. The Wolffian duct on the left side, which can be traced as a patent tube for some sections above the level mainly concerned in the description just given, can be seen to come into direct contact, lower down, with the outer aspect of the left lateral vaginal bulb, but without in any way participating in the formation of this structure. Fig. 7 gives the serial sections in which this occurs, and it can be seen that the remnant fades away without any sign of epithelial activity or bulb formation at its lower end. This is the only example we have in our specimens of a Wolffian duct coming close to, or in contact with, the Müllerian cells, and there seems to be no reason to doubt that the condition in this case is an accidental combination of a localised irregular growth of vaginal cells with a persistent Wolffian remnant.

It will be remembered that it was shown in earlier specimens that the utero-vaginal canal comes into contact by its epithelium with the upper and posterior wall of the urogenital sinus. It is by means of the vaginal bulbs which have now been mentioned, that this area of contact is maintained and increased, the vaginal cells pushing their way, by this proliferation, downwards along the posterior wall of the sinus.

Formation of the vaginal bulbs progresses steadily, and, by the stage of 110 mm., has reached considerably greater proportions and more complicated appearance than in former specimens, without yet attaining that exaggeration

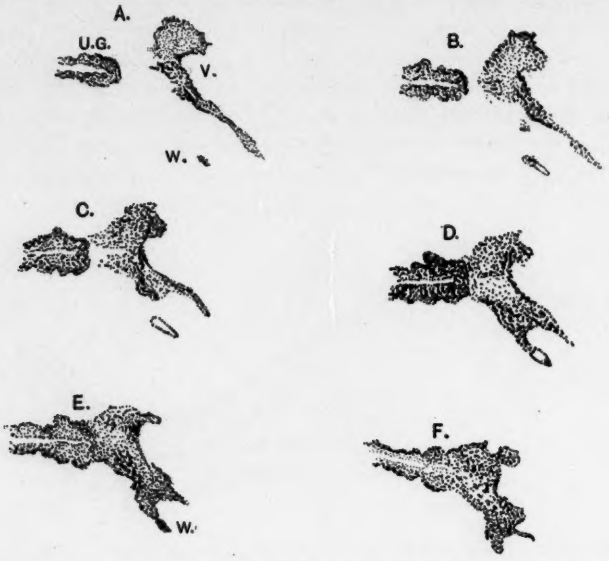


Fig. 7. Successive sections, 79 mm., to show a Wolffian rudiment (*W.*) in contact with the Müllerian vagina, *V.* *U.G.*, urogenital sinus. The rudiment enlarges in C., but its wall remains a single-celled layer. It comes into contact with the vaginal mass in D. and begins to fade in E. Sections 15$\mu$.

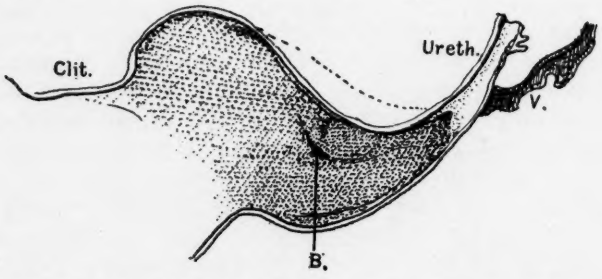


Fig. 8. 110 mm. Reconstruction of sinus. Sagittal section. *V.*, vagina; *B.*, orifice of duct of Bartholin's gland.

of growth which marks the later stages. As in the earlier specimens, this epithelial proliferation is associated with the triradiate shape of the mass, on section, already alluded to, and the anterior central portion reaches and

establishes contact with the upper and posterior part of the sinus wall. There is no evidence whatever of any intervention of Wolffian duct or bulb.

After this there is a progressive actual and relative increase in size of the lower end of the utero-vaginal canal. The general nature of this growth has been indicated in the description given above, but may with advantage be repeated here with some additional details. Just above its lower end, the lumen of the canal is occluded as the result of the activity of its lining cells (fig. 9). As it is followed down, this activity is seen to become concentrated mainly in three "centres," a single median and two lateral, and the three "vaginal bulbs" formed in this way project into the surrounding mesoderm

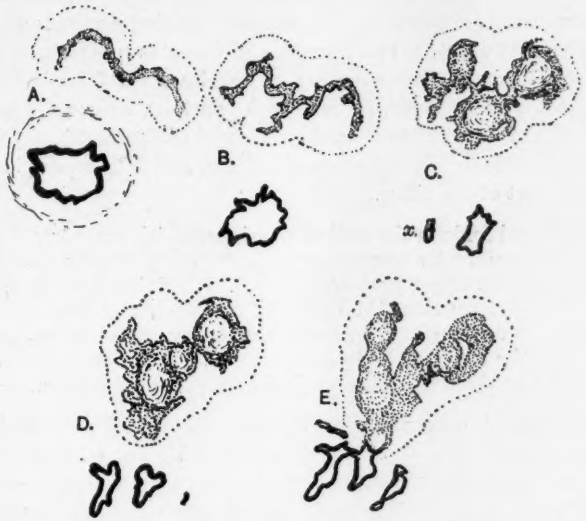


Fig. 9. Several sections showing the enlargement, from above down, of the lower end of the vaginal structures, 135 mm. The three main bulbs are seen in C. *x.* is the upper end of a recess of the sinus.

as rounded masses possessing vacuolating centres. The anterior or median bulb is in contact with the posterior sinus wall, invaginating it slightly and thus producing a low projection of vaginal epithelium covered by the lining cells of the sinus. At the apex of this projection the cells are breaking down, allowing communication between the sinus and the cavity which is appearing within the bulbs as a result of the disintegration of their central cells. This marks the site of the hymeneal orifice—limited for the moment, of course, in extent—while the area of contact of vaginal and sinus cells forms the upper central part of the hymen, just below and behind the urethral orifice.

That this appearance, becoming more evident and important as development goes on, is the result of a true invagination and infolding of the posterior

wall of the sinus, and not merely produced by a growth of this wall to keep pace with the bulging epithelial vagina, is shown by the altered relation of the hymeneal site to the various grooves on the lateral wall of the sinus.

The configuration of the lateral wall has already been briefly noticed, and one groove in particular—that into the depths of which Bartholin's duct opens—has been pointed out. As development proceeds, the relief of this wall becomes more complicated, with the formation of additional grooves and folds. Certain grooves, however, can be found at all stages, and among these is that just mentioned as receiving the duct of Bartholin's gland. The gland and its duct remain in the same relation to each other, the gland deeply fixed in surrounding structures, and the duct running upwards and forwards from it. The duct aperture can therefore be taken as maintaining a constant position in the sinus, and affording a definite level from which relative measurements may be made. It will be found that, as growth goes on, the duct opening and the hymeneal level get nearer: as the duct is fixed, it follows that the hymeneal level is being brought down, and this implies invagination of the upper part of the sinus.

The additional folds in the wall of the sinus, which appear as development proceeds and seem to be somewhat variable, are probably associated with this inturning of the upper part of the sinus. It is interesting to observe that they appear higher up than the orifice of the duct, and that there is a tendency to the formation of a groove in a transverse plane as growth goes on, just below the level of the hymen, where in fact such a groove might be expected to form with increasing vaginal pressure from behind.

As development proceeds, we find the vaginal bulbs—and, to a lesser extent, the whole vagina—growing at a rate quite out of proportion to the growth of neighbouring structures. This can be shown by comparing the two stages, 135 mm. and 170 mm., in fig. 10. The reconstructions were made at the same magnification, and the vaginal formations in the older specimen are enormous compared with those in the earlier one: yet the urethrae are little different in size and the differences in the sinus are only in proportion to the general increase, although this point is not very evident in the figure, only a small part of each sinus having been modelled.

Fig. 11 gives the sagittal section of the parts in the 170 mm. specimen. The magnification is, of course, much less than in the figures already given of one or two earlier stages, but, bearing this in mind, it is evident at once that the orifice of Bartholin's duct (*B.*) is much nearer the hymeneal level than in those stages (figs. 6, 8). In other words, the invagination of the wall of the sinus has progressed considerably in connection with the great growth of the vaginal bulbs. The line of inflection, along which the wall is invaginated to form the covering of the hymen, is indicated by the interrupted line *Y*. Thus the distance from *B.* to *Y.*, *plus* that from *Y.* to the crest of the hymeneal prominence, is the distance between the Bartholin site and the posterior wall

of the sinus of the earlier stages, modified now (see also fig. 12) by progressive in-folding.

At *a.*, below the bulbs, are certain diverticula or prolongations from the sinus: these can be seen also in fig. 11, and seem to be associated with the invagination.

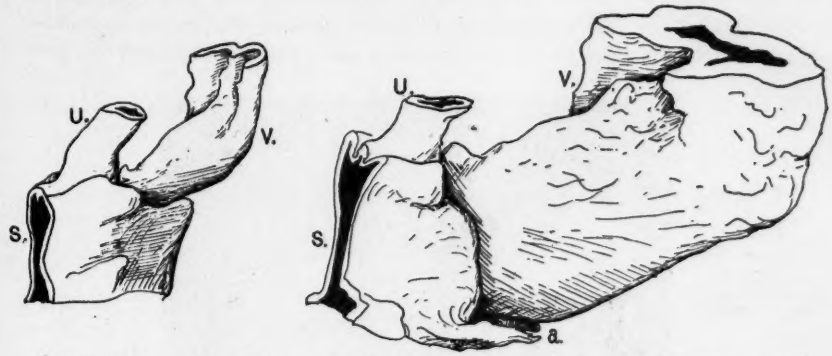


Fig. 10. The lower end of the vagina (*V.*) at 135 mm. compared with one of 170 mm., showing the relatively enormous growth. Drawn from models made at the same magnification. *S.*, part of the sinus, invaginated above and behind by the vaginal growth; *U.*, urethra. The "outgrowths" from the sinus below the bulbs are indicated at *a.*

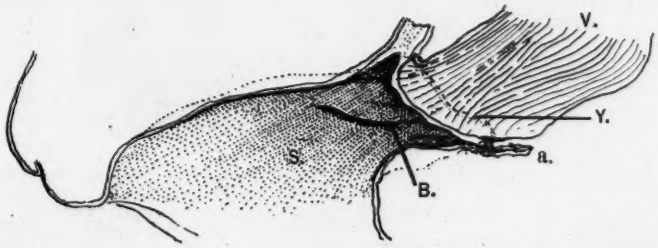


Fig. 11. Sagittal section, 170 mm. Reconstruction. *B.*, Bartholin's duct; *Y.*, line of inflection of wall of sinus, *S.* Outgrowths (?) are shown at *a.*

These were noticed by Mijsberg, who looked on them as active outgrowths. This was, to some extent, also our view so far as their extremities, at any rate, were concerned, but we have the impression that in their greater part they are probably only side-effects of the invagination: the question, however, is not easy to solve, and it is fortunate that it does not appear to be of primary importance.

This 170 mm. specimen presents conditions so suggestive and important for the present study, that further consideration of it is pardonable. It has been seen that the very large bulbous end of its vagina has markedly invaginated the posterior wall of the sinus, and this leads to a somewhat cone-shaped projection into this cavity (fig. 12). This receives a covering of the

lining cells of the sinus on its surface. The central cells of the vagina are breaking down, and the cavity so formed communicates with that of the sinus at the apex of the projection, so marking the site of the hymeneal opening. The basic structure of the hymen is seen in fig. 12, where the central portion of the upper part of that structure is already made. It is seen to consist of cells derived from the vaginal epithelium, covered superficially by sinus epithelium, and possesses an intervening layer of vascular mesoderm derived from the condensations round the walls of the cavities.

Fig. 12. Section, 170 mm., showing invagination of wall of sinus by vaginal bulbs, with formation of hymen. In the process the lower end of a persistent Wolffian duct, *W.d.*, has been turned in and opens on the hymen. The composition of the hymen is also seen, as well as the cellular conditions within the vagina.

One of the most interesting features of this specimen is the presence of a Wolffian duct on one side, which reaches the sinus and extends for a considerable distance upwards beside the vagina. The lumen of this rudiment is small but clear, and is surrounded throughout by a single layer of cubical cells, there being no indication whatever of any cellular activity in the direction of division or hypertrophy: the layer is only a persisting simple lining layer. When followed down, the duct, embedded as in all cases in the lateral part of the thick condensation surrounding the vagina, is found to open on the surface of the hymen (fig. 12, *W.d.*) a little distance from its "free border" or opening. It is evident that that part of the wall of the sinus on which the duct originally opened has been invaginated, turned in by the growth of the vaginal bulbs behind it, and has thus come to form part of the superficial

aspect of the hymen. Lastly, it has to be noted that the Wolffian tube nowhere in its course shows any sign whatever of contact or fusion, past or present, with the vaginal epithelium, nor (as has been pointed out) is there any smallest indication of past or present bulb-formation about it: it is a separate structure, not concerned with the activities in progress in the vagina, and its presence in this case is a happy accident which in its conditions bears out to the full the inferences drawn from examination of stages in which no such rudiment was to be found.

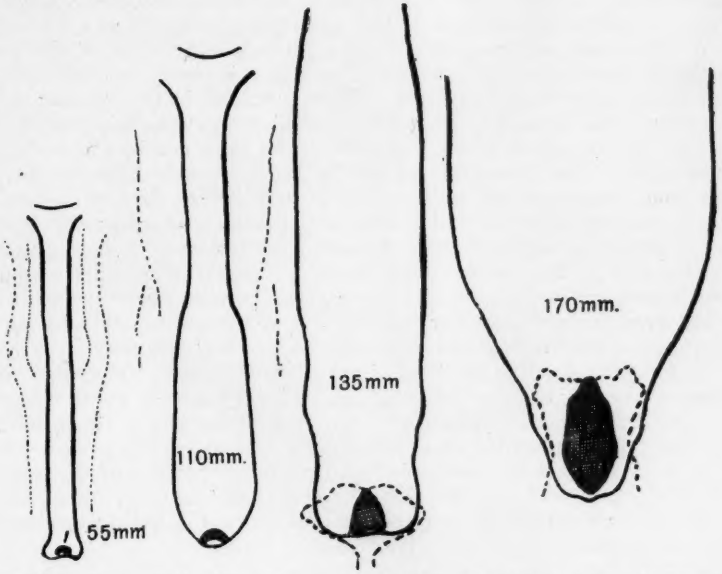


Fig. 13. Schematic reconstructions. The utero-vaginal length is shown in the first two diagrams the vagina only in the third, and its lower portion only in the last. The area of contact with the sinus is shaded, and the outline of the neighbouring part of the sinus given in interrupted lines. Magnification the same in all.

The relatively enormous bulbous growth in this foetus is only the modified representative at the lower end of the vagina of a disproportionate increase in size found in the canal above this. The striking size of the bulbs in fig. 10 would be lost to a large extent if they were viewed from behind, for there is marked side-to-side compression. The vagina higher up, on the other hand, is widened laterally to a considerable degree and compressed from before backwards. Fig. 13 represents these relations by schematic reconstructions of four stages: it can be seen that, whereas the increasing vaginal breadth in the first two stages does not markedly exceed a growth proportionate to the general increase, that of the 170 mm. stage is quite disproportionate. At the same time the lower end, at first wider than the rest of the tube, becomes

relatively narrower. This is associated with the beginning of bulb-formation, these structures being compressed laterally: subsequently they extend downwards by their continued growth and in so doing increase the area of contact with the wall of the sinus in a downward direction.

The bulbs show, centrally, large rounded vacuolated cells staining poorly, which are disintegrating, while the more externally placed cells are small and stain well, and are apparently growing rapidly and pushing their way into or within the surrounding mesoderm. A question arises at once as to the source of these cells, but there does not seem to be any reasonable doubt about the matter. Apart from the fact that this epithelial plug exists at a time when the Wolffian ducts are present and open separately in the sinus, we have seen that in all the subsequent stages mentioned in this paper there has been no evidence or suggestion of any sort of bulb-formation in the Wolffian ducts, when these could be traced, and, *a fortiori*, no hint of any participation of these ducts in the formation of vaginal bulbs. The same can be said about the suggestion that the cellular bulbs might be derived from the urogenital sinus: the vaginal structures are solid masses of cells before the blending of the respective epithelia occurs, and in none of our sections of later stages is there any appearance of ingrowth from the sinus, but rather of vaginal projection into this cavity. The utero-vaginal canal and the Wolffian duct remnants, when present, are surrounded by a condensation of mesoderm which is directly derived or continued from the condensation of the genital stalk. With the appearance of the bulbs, it has to be decided whether their form is the result of a high degree of activity of the vaginal cells, or is due to an invasive action of the surrounding cellular condensation. When we see the relative increase in size of the two contrasted regions, and observe the way in which the condensation layer is moulded on the contained vaginal growth, there seems no reason to doubt that the former is the correct explanation. If the irregular bulbar outline were due to invasion by the surrounding cells, one would not expect such altered shape and accommodation to the bulbar outline, but rather the maintenance of the original regular form.

The method by which the lower end of the vagina is formed and its area of contact with the wall of the sinus is enlarged, as we have described it in this paper, progresses up to birth at least, and the increasing invagination of the upper and back part of the sinus wall causes an increase in size of the hymen and brings it nearer to the surface. Fig. 14 shows the condition in a specimen of 240 mm.; this is enlarged only half the amount of the 170 mm. foetus in fig. 11, but comparison of the two figures will show at once how much progress has been made in the growth of the bulbs and in the invagination. This last process has gone on to such an extent that the orifice of the duct of Bartholin's gland is now hidden by the projecting hymen, and is not very far from the base or line of inflection of the hymen: it is interesting to observe, in this foetus, that the upper end of the long groove, into the depths of which the duct opens, reaches and is turned down on the side of the hymen.

The second section shown in fig. 14 is that of a foetus at full term, in which the orifice of the duct is close to the base of the hymeneal inflection.

It shows the final foetal stage of the invaginating process which was initiated some four or five months previously.

There are many matters and questions associated more or less closely with the development of the vagina which have not been mentioned, or at most very shortly—such as the development of the urogenital sinus, the changes occurring in the growths from this, the formation of the urethra, the extension of condensations, etc. We have purposely refrained from introducing these subjects, leaving them for further consideration at a future time, and have

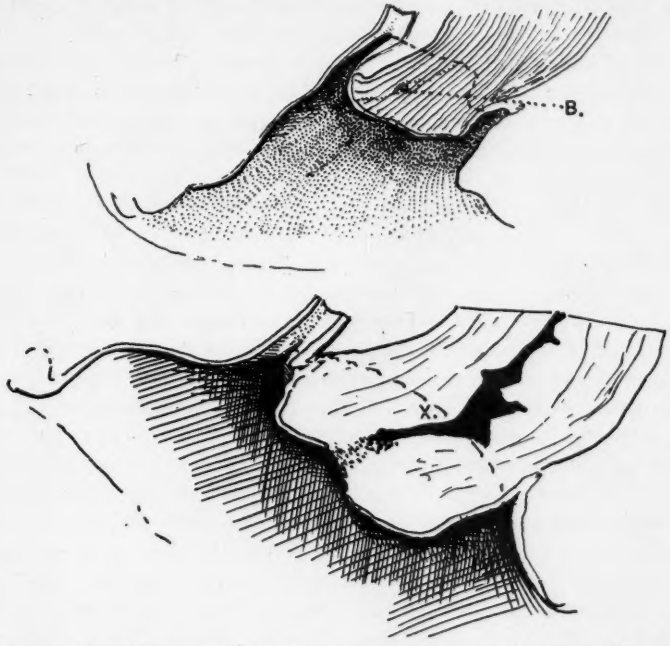


Fig. 14. Sagittal sections of (above) 240 mm. foetus, and (below) foetus at term, at similar magnification. *B.* and *X.* indicate the situations of the openings of the ducts, deep to the hymeneal projection.

endeavoured to confine ourselves to the main general question—the origin of the lower end of the vagina, and the mode by which it attains the position of its final opening—without going into details which are not essential.

The views which we hold, as the result of our observations on the material, may now be briefly summed up. They are as follows:

1. The lower end of the vagina, like the rest of that structure, is purely a Müllerian derivative.

2. It establishes contact with the urogenital sinus at an early stage, at the apex of the "Müllerian tubercle." This site is that of the upper part of the future hymen.

3. Its lumen is for a time filled up by a plug of epithelial cells, derived from the lining cells of the canal. Later, by their active growth, these cells lead to the formation of the so-called *vaginal bulbs*. These bulbs increase the area of vaginal contact with the sinus (and become the hymeneal area) by their extension in a downward direction along its posterior wall. At the same time they invaginate this wall from behind, so that the sinus undergoes a relative diminution in length and a change in direction of its long axis, a corresponding increase occurring in its opposite diameter. The hymeneal site is thus made to approach nearer the surface.

4. The hymen is formed passively by the invagination of the posterior wall of the sinus, as just described. Thus it consists of three layers—a layer of vaginal cells from the invaginating "bulbs," a covering layer of epithelium from the sinus, and an intervening stratum of vascular mesoderm which appears to be derived from the vascular condensations surrounding the walls of both these cavities.

5. The Wolffian ducts take no part in the formation of any portion of the vagina and hymen. They disappear in their lower parts (as a rule) at a fairly early stage, and, when persistent, can be followed as patent small tubes which open near the free border of the hymen. This position on the hymen is due to their terminal openings being invaginated with that part of the sinus wall in which they are situated, and any secondary change leading to an opening beside the hymen would evidently be due to disappearance of the thin covering of sinus cells which lies over their invaginated ends.

In comparing these results with those of other observers we are faced with the difficulty of classifying the diverse opinions for purposes of review. It is only possible to do this in a very general way, owing to the overlap in many details, and perhaps the large division into three main classes, which we mentioned earlier in this paper, affords as good a basis as any, on which we can make the comparison. These three headings were:

(*a*) Descriptions which give the derivation of vagina and hymen as purely Müllerian.

(*b*) Those which make it mainly Müllerian, but bring in an additional element in the development of its lower part. This new factor may be derived from the Wolffian ducts or from the urogenital sinus, entailing an associated origin for the hymen.

(*c*) Those which derive the vagina mainly or altogether from the urogenital sinus, with similar hymeneal origin.

The difficulty of placing any individual opinion in its proper class can be exemplified in the present case: the views we advocate would certainly seem to belong to class (*a*) in the list just given, but, strictly speaking, the sinus-element in the hymen would give some reason for placing them also in (*b*).

(*a*) R. Nagel(1, 2) is one of the main supporters of the entirely Müllerian origin of the vagina. He described it as arising wholly from the united Müllerian ducts, the lower ends of which, becoming solid, grow rapidly in

length through hypertrophy and multiplication of their lining cells, and come to invaginate the posterior wall of the urogenital sinus. The apex of the projection so formed breaks down to allow communication between vagina and sinus, this marking the site of the future hymeneal orifice—in the position of the Müllerian tubercle of earlier specimens. In this way the lower solid portions of the Müllerian ducts form the vagina, a lumen being absent throughout. This view, it is evident, is, in essentials, the same as that which we put forward, as is also his description of the formation of the hymen, which he considers to arise passively by the bulging of the Müllerian vagina into the sinus, invaginating it. He considers that *active* growth of the hymen may take place later, as shown by the fact that the hymeneal orifice may be relatively smaller in the new born child, than at a period in foetal life. This is, however, difficult of proof, and does not affect the main issue as to the mode of development of the hymen. While Nagel describes a bulging of the lower end of the vagina, the vaginal bulb-formation, which is so striking in our specimens, is not mentioned, nor the process of spread of the vaginal area of contact with the sinus, brought about by this means.

Wood Jones (3) describes this Müllerian downgrowth as double, and in the form of bulbs. According to him, the fused Müllerian ducts reach and open into the upper end of the sinus at a comparatively early stage. Later this opening is lost, to be regained at an advanced stage of foetal life, this second opening being brought about by a paired bulbar downgrowth from the fused Müllerian ducts. These bulbs tunnel their way along the mesoderm behind the posterior sinus wall, to open at a much lower level than the primary opening, the hymen being that part of the mesoderm lying between this paired bulbar downgrowth and the surface, and at first unaffected by it.

While this view is distinctly comparable with ours as here expressed, we should like to say that we have never in any of our specimens seen any trace of a paired downgrowth in the mesoderm posterior to the sinus and not in contact with its wall. Wood Jones does not make it clear, when he states that the primary opening between vagina and sinus is lost, whether an epithelial contact is maintained, but we take his meaning to be that all communication between the two channels and their epithelia is lost, an opinion which we have found by our specimens to be erroneous. Contact having once been established between the vagina and sinus, at the 30–38 mm. stage, is never again lost, but continues to increase in area by the formation of the vaginal bulbs and their downgrowth along, and in contact with, the posterior sinus wall.

According to other authors (with whom we do not disagree) the original utero-vaginal canal takes a much larger share in the formation of the vagina, which possesses at first a lumen, lost through transition of the simple lining epithelium, into a multilayered squamous epithelium, the lumen of the canal being lost through growth of its anterior and posterior walls.

Felix (4) describes this epithelial transition also, mentioning the appearance

here of large rounded cells, which fill up the utero-vaginal canal and render it solid. The origin of these cells has caused much speculation, Felix considering that they arise from the cells lining the Müllerian ducts, while Berry Hart (5, 6) derives them from the so-called *Wolffian Bulbs*, and Van du Hoeven, as quoted by Mijsberg (7), derives them from the lining membrane of the urogenital sinus. This places the views of these last two observers in our next group (*b*).

Before passing on to consider this group in detail, a few further remarks must be made on the "*vaginal*" view of the origin of the *hymen*.

Taussig (8, 9) in his original paper bases his views on five embryos examined by serial section, and considers the hymen has a *vaginal* origin independent of the place at which the vagina breaks into the urogenital sinus. Within this latter site arises a fold of vaginal tissue, the hymen. At the point where the vaginal bulbs break through, i.e. at the Müllerian tubercle, another more or less well-marked fold of tissue is left, which becomes obliterated as development proceeds. Taussig thinks that the bi-lamellate *utero-vaginal hymen*, which Schaeffer (10) describes as being found in so large a proportion of his specimens, is due either to an abnormal persistence of these two folds, or to the fact that many of the specimens were examined at a stage when both folds would be normally present.

Taussig in a later paper (9) states that the hymen is not a passively formed structure, but that it is an actively proliferating outgrowth, and considers that such variations in the normal hymen as *hymen cribriformis* can only be explained on such an hypothesis. We consider that such a variation as a cribriform hymen, could very readily arise by a process of passive bulging of the posterior sinus wall by the actively bulging vaginal bulbs, rupture and communication of the two contiguous lumina taking place not at one point but at several, on the apex of the epithelial covered promontory so formed.

Taussig's second paper is largely based on vaginal and hymeneal abnormalities and, as these will be discussed later, nothing further need be said now about them.

Blair Bell, when asked to discuss Taussig's (9) view, stated that he considered the hymen to be the remains of the urogenital plate, or anterior portion of the original cloacal membrane, but considered the question not proven as to whether it were a new formation or a disappearing membrane.

Gellhorn (11) is in agreement with our view and with that of Nagel, that the development of the hymen is inseparable from that of the vagina, and is formed by a bulging of the *vaginal bulbs* into the sinus. He, however, derives practically the whole hymen, with the exception of a thin epithelial covering from the sinus lining, from the vagina, considering that mesoderm from the vagina only grows into this. We are of the opinion that a true *ad hoc* invagination of the posterior sinus wall occurs, and that the *mesoderm* of the hymen is derived both from that of the vagina and of the urogenital sinus.

We have never seen any evidence of a *vaginal* hymen, arising as an active fold of mucous membrane, and consider that the microscopical appearances

are quite against such a view. The lumen of the lower end of the vagina (i.e. in the region of the vaginal bulbs) is filled with vacuolated desquamating epithelium, all activity of growth taking place at the outer limit of the epithelial mass, towards the surrounding mesoderm and the urogenital sinus.

Among the more recent observers whose views must be placed in this class, are Küstner (12) and Lubosch (13). The former considers that the hymen arises at the site of the early Müllerian tubercle, taking as proof of this the fact that, where the Wolffian duct is persistent, it opens on the hymen, i.e. its original site in embryonic life. His paper is largely based on a study of abnormalities, and he considers that such an error of development as the presence of the hymen in the absence of vagina is rather against his views expressed above. He states, however, in this connection, that the hymeneal relations vary with the degree of development of the Müllerian ducts.

Lubosch (writing in Halban and Seitz's text-book of Gynecology) describes the formation of a bulging lower end of the vagina, which invaginates the posterior wall of the urogenital sinus, the hymen thus coming to be formed passively, as we have described in our paper. He describes, however, the limiting of the spread of the bulging epithelial vagina, by a ring-like narrowing, which is continuous with the columnae rugarum and which he calls the "plica retrohymenalis." We have remarked no such specialised structure in our specimens.

We now come to the second class (*b*) of hypotheses about the development of vagina and hymen, namely that the former is mainly a Müllerian structure, but an additional factor is present in its formation and in that of the hymen.

(*b*) Berry Hart (5, 6) is one of the best-known exponents of this view. He considers that the upper two-thirds of the vagina arises wholly from the fused Müllerian ducts, while he ascribes to the "Wolffian bulbs"—i.e. the lower ends of the Wolffian ducts, which he describes as becoming solid and developing bulbar enlargements on their extremities—the formation of the lower third of the vagina, the lining membrane of the entire vagina and the hymen, which therefore, in his opinion, forms below the site of the former Müllerian tubercle, i.e. at the original site of entry of the Wolffian ducts into the urogenital sinus.

Before proceeding to show how entirely we disagree with this view, those of some other observers, holding somewhat similar opinions, must be examined.

Tourneux and Legay (14) also mention the presence of "Wolffian bulbs" and consider they form the lower third of the vagina.

Mijsberg (7), whose recent and most interesting paper was published while this research was in progress, is of the opinion that the upper two-thirds of the vagina is Müllerian while the lower third is formed by the fusion of the Wolffian bulbs with each other, with the Müllerian vagina above, and the sinus below, while the hymen forms as the result of the reaction of the sinus to the growth in length of the vagina—here, in a limited sense, in agreement

with our view—and is therefore in actual structure, according to Mijsberg, partly of Wolffian and partly of sinus origin.

Against these views the very definite evidence of our specimens and reconstructions must be placed. At no stage and in none of our specimens have we seen any evidence whatever of Wolffian bulb-formation. In many of our specimens it was possible to trace the Wolffian duct to a lesser or greater extent. In the former case, with one exception, the Wolffian duct was always lost sight of as a patent duct, possessing a lumen, lined by a single layer of cubical epithelium, and without any evidence of proliferation of these lining cells or of bulb-formation. In the exceptional case, the Wolffian duct was seen on one side to join, or rather come into contact with, the outer side of the Müllerian bulb-formation. No cells, however, were given from the Wolffian duct, to this bulb-formation, which had already reached a developed state above the level of contact, and the duct was completely lost sight of in the next—serial—section. In cases where the duct could be followed to the sinus its lumen was maintained throughout, and it opened into the urogenital sinus below the opening of the fused Müllerian ducts. This is particularly well seen in one—170 mm.—specimen, where a patent Wolffian duct on either side is seen to open into the sinus on the surface of the hymen. R. Meyer (15) has also traced the duct opening in this position.

In addition, against the view put forward by Berry Hart—that the hymen forms below the site of the original Müllerian tubercle—we consider that we have conclusive evidence in our specimens and the reconstructions made therefrom, that the fused Müllerian ducts, having once established contact with the sinus epithelium at the apex of the Müllerian duct, never again lose that contact (and at this site the hymen is formed) but continue to increase it, and the area of the hymen, by the formation of the Müllerian or vaginal bulbs.

Other workers who in addition to R. Nagel, already quoted, agree with us in attributing a "unilamellate" vulvo-vaginal origin for the hymen, are Budin (16) and Webster (17). Budin, basing his work on dissections of adult specimens, considers that the hymen does not exist as an independent structure, but that it is merely the projecting lower and anterior end of the vagina, while Webster describes the hymen as the septum which is left between the urogenital sinus, and the lower part of the vagina, as the latter becomes channelled, the opening of the hymen being formed by the involution of the epithelium on the urogenital surface of the hymen.

Spuler (18) considers the vagina mainly Müllerian, but thinks that the lower fused ends of the Müllerian ducts, here called the "Conus Vaginalis," derive cells from the urogenital sinus, and that the lower third of the vagina arises by a frontal division of the urogenital sinus, which brings this worker into line with the next group, (*c*), in which the sinus is held to play a large and important part in the development of the vagina.

(*c*) Retterer (19) describes lateral folds arising in the sinus wall, about the

fourth month of foetal life. By union of these folds from above downwards, the lower portion of the vagina is formed, the upper part, i.e. that in relation to the base of the bladder, being formed from the Müllerian ducts.

Pozzi(20) also agrees that the lower third of the vagina is derived from the urogenital sinus.

The latter bases his belief largely on a study of vaginal and vulvar abnormalities, especially on a case in which a hymen was present but no vagina. The vagina was represented by a small pocket only, which he considers to be the lower part of the vagina, derived from the urogenital sinus, which also gives rise to the hymen. Other abnormalities of development put forward to support this view are:

(1) The presence of a single hymen with a double vagina.

(2) The presence of a hymen or fold which surrounds urethral as well as vaginal orifice.

On the general question we would like to point out that theories of development based on mal-developments are only satisfactory when the assumptions are borne out by normal embryological investigation. At least, they should not be in opposition to what is observed in normal development. It is not usual to find the hymen in the absence of the vagina, but there is nothing in its presence under these conditions to invalidate or disprove in any way the facts observed in the study of a normal sinus. The urogenital sinus has many folds, and these can be followed from their inception to what is practically the attainment of the definitive condition, but we have certainly not seen any stage, nor have we been able to come across any description, in which one or more of these folds is clearly shown to form a hymen. On the other hand, the hymen can be seen to be formed at the contact-region of vagina and sinus. It would seem much more likely that, in these cases, the lower end of the vagina and hymen were made in the way indicated above and that subsequently and for some reason in any case unknown, vaginal atrophy occurred. So far as we know, no dissection has been undertaken on such an abnormality to determine the presence or absence of remnants of a vagina.

With regard to the second abnormality, double vagina and single hymen, this would seem to admit of a very simple explanation. The double character belongs to the vagina, and, as has been shown, is still evident to some degree at the lower end, even when this is growing. Nevertheless, the growth, as a whole, invaginates the wall of the sinus and produces the hymen, and it does not require much imagination to see that it is quite possible for the double character of the vagina to be much more marked and persistent, while the effect of the growth of the structure, as a whole, is exercised in the production of a practically unpaired projection into the sinus. Still more marked division, or want of fusion, of the vagina, and distinction of its bulbs, would lead to a definitely double invagination, from which would be derived the commoner variety of double hymen with double vagina.

The presence of a hymen surrounding the urethral orifice as well as that of the vagina does not appear to invalidate in any way the account given of the formation of the parts. In fact, during the course of this investigation, we have noted with interest the presence of a definite invagination of the posterior and upper part of the sinus wall implicating the urethra as well as the vagina. In this way a common hymen might be formed, although, as a rule, the structure ultimately becomes vaginal. We have made some observations on this matter, but have not paid particular attention to the details, as they seemed to be rather outside the more fundamental scope of the questions we were trying to solve. An investigation of the whole development of the female urethra, particularly of its lower part, is needed: we did not go into the question, but what we observed has satisfied us that the presence of a hymen which includes the urethra may be an indication of an inhibition, but at any rate does not clash with the vaginal productional value of the ordinary hymen.

With regard to Retterer's view, we know that septum formation and division of the sinus are said to occur in certain animals (Mijsberg(7a)). We have not studied these, and are of course in agreement with most other observers, that such a method of development never takes place in the human embryo. The site of the opening of the Wolffian ducts into the sinus below the Müllerian vaginal orifice, disproves this theory. If the lower third of the vagina arose from the sinus, the Wolffian ducts should open into the vagina—unless indeed, as suggested by one author, they deviate from their close relation to the vagina at this point, extend down in the mesoderm external to the sinus, and come to open below the vaginal orifice formed as above. It seems hardly necessary to say that this effort of the imagination lacks any support whatever from developmental observation.

Before bringing this account to an end, we would like to call attention once more to the Wolffian ducts. On general principles one would expect to find the female tract associated with the Müllerian ducts, but, on some views as to their possible evolution, it does not seem justifiable to deny theoretically the possibility of some Wolffian intervention at the lower end. With such outlook we naturally paid particular attention to the nature and condition of any remnants of the Wolffian ducts with which we came in contact. In this matter we were struck by one common character possessed by all these remains: there was never any sign whatever, in any place, of any activity of the lining cells of the ducts. Their lining was formed by a single layer of cubical cells, surrounding a small lumen, except in those sections where the lumen was disappearing, the cells here coming into contact and getting smaller, and the whole structure plainly on the point of vanishing. In fact the only signs of activity seen were retrograde and directed towards atrophy and disappearance. At no time could we see the faintest sign that either duct might be about to form a bulb, was forming it at the time, or had formed it, and, whenever that duct could be traced to the sinus, it ran to its original site

without any enlargement, and unconnected with the vaginal structures. We have spoken of the one case (fig. 7) which seems an exception to this last statement, but the fact that it was the only case, and the appearance presented by the remnant on examination, make it in our opinion clearly a case of accidental contiguity. Here and there, along the sides of the vaginal bulbs, are processes directed outwards and backwards, which owe their direction doubtless to the fixation of their ends in the surrounding condensation while their bases are carried forward by the growth of the bulbs. Such processes, when cut longitudinally, may be taken—in our opinion—for Wolffian remnants, and we cannot help thinking that some such mistaken reading of a section may account for some of the descriptions of "Wolffian bulbs[1]." The fact that they may be fairly numerous, and that they may co-exist with the real duct, disposes of them at once. The successive stages that we have examined have given us pictures in which the outstanding impressions we have gained have been those of great activity in the Müllerian structures, and complete absence of activity of any sort, except atrophy, in the Wolffian ducts.

## SUMMARY

1. The subject was investigated on human material only, by means of serial sections.

2. The Müllerian ducts, fused, reach the wall of the urogenital sinus between 30 and 38 mm. (probably a little variable).

3. Slowly, after this, the lower end of the vagina begins to grow, thus enlarging the originally small area of contact with the wall of the sinus.

4. The growth is due to multiplication of vaginal cells, and is already evident before the end of the third month. It progresses slowly, assuming the form of "vaginal bulbs," paired structures fused in front with a common median swelling. These are well formed by the fifth month, and now begin to grow much more rapidly.

5. The bulbous growth of the lower end of the vagina is particularly effective in two directions: (*a*) it pushes in the posterior wall of the sinus, invaginating it into the cavity, and (*b*) it extends down along this posterior wall, thus increasing markedly the contact area between vagina and sinus.

6. The progressive invagination of the wall of the sinus makes this cavity relatively shorter: this seems to go on up to birth at least.

7. The hymen is produced by the meeting of vaginal and sinus structures, and therefore corresponds with the area of contact, and increases with it. It bulges into the sinus as this area is invaginated; its lower surface is made by the invaginated wall of the sinus, its upper surface by evaginated vaginal cells, and a vascular mesoderm partly separates these.

[1] I remember seeing the drawing of a section many years ago, where such a projection was labelled "Wolffian." I remember the section clearly, although I cannot recall the paper, and at the time I wondered—without doubting—on what grounds it was recognised as Wolffian. I concluded that the writer had inside information on the matter, but I am inclined now to think he was simply mistaken. (J. E. F.)

8. The central part of the area of contact, where there is no intervening vascular layer, breaks down, and the cavity of the sinus thus has opening into it the cavity of the vagina, made by breaking down of the central cells of the bulbs. The opening thus made is the hymeneal orifice.

9. The duct of Bartholin's gland, at first far down in the sinus, gets relatively higher and higher. This is not due to any change in position of the duct, but to the increasing invagination shortening the sinus from above, and bringing the hymen to an increasingly lower level. Finally, the upper part of the long groove into which the duct opens is turned down on to the side of the hymen, and the duct comes to open near its margin.

10. The Wolffian ducts take no part in the formation of the vagina and hymen. They usually disappear. If they persist their lower ends are invaginated, and open on the hymen: secondary degeneration of their walls may lead to a persistent opening being situated beside the hymen.

11. Published views on the formation of the parts have been shortly summarised and considered, with the possible bearing of certain malformations.

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# THE FACIAL MUSCULATURE OF THE AUSTRALIAN ABORIGINAL[1]

## PART II

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## DESCRIPTION OF THE FACIAL MUSCULATURE OF D. B. 2, AND A COMPARISON OF THE FACIAL MUSCULATURE OF THE AUSTRALIAN ABORIGINAL WITH THAT OF OTHER RACES

### Platysma

(1) Nape platysma. This was not present.

(2) Neck platysma. This is well developed and belonged to Bluntschli's Type III, and its fibres are equally well developed in both neck and face in contrast to H. B. 1. Bluntschli divides this portion of the muscle into a pars aberrans and a pars labialis.

The pars aberrans fibres turn oralwards and they end by interlacing with the fibres of the caput buccale M. triangularis (M. risorius Santorini). A few fibres proceed vertically to end in the fascia covering the parotid gland.

The pars labialis (Bluntschli) has three different points of attachment: (*a*) the modiolus, (*b*) the lower lip, and (*c*) the mandible. Hence arise the terms portio modialaris, portio labralis, and portio mandibularis.

*Portio labralis.* The portio labralis extends to the middle line mingling with the M. quadratus labii inferioris fibres. A broad band (0·8 cm.) of the labral platysma passed to the lower lip, deep to the most lateral attachment of the caput longum M. triangularis, and was bridged over by the whole of this muscle. (This broad band extended laterally to within a few millimetres (5–6) of the angle of the mouth, i.e. somewhat more lateral, than in H. B. 1.) The remaining fibres pass between the fibres of the caput longum M. triangularis, at its bony origin.

*Portio mandibularis.* This is inserted into the lower border of the mandible from the middle line to a point 5·5 cm. lateral to it. There was no bony attachment of the platysma lateral to the attachment of the caput longum M. triangularis.

### Musculus nasalis. Pars transversa

The fibres of the pars transversa are inextricably mixed with those of the caput angulare M. quadratus labii superioris at the cranial end of, and above the naso-labial furrow. It is a well-developed muscle, and has the normal

[1] Part 1 appeared in this Journal, 1926, vol. LXI. p. 14.

origin inferiorly. From this area of interlacement, the fibres can be traced on to the bridge of the nose. This sheet on the bridge of the nose extends inferiorly from a point in the median line of the nose which is 1·5 cm. below the lower border of the nasal bone. From this point to the lower border of the nasal bone, the pars transversa continues into its fellow of the opposite side. The muscle has the typical sphincter-like arrangement in relation to the post-vestibular part of the nose.

The pars alaris seems to have the usual arrangement, the lateral fibres going to the ala nasi, and the medial fibres to the septum and septal cushion.

*Muscle alaris.* Traces of a M. alaris were present.

No trace of a M. apicis nasi was found.

### Musculus quadratus labii inferioris

This is well developed, completely covering the chin, as far as the pogonion, and its fibres are directly continuous with the fibres of the labral platysma. It, and the labral platysma, completely hide from view the pars peripheralis of the M. orbicularis oris. Its origin extends from within a few millimetres of the middle line as far laterally as the lateral limit of the M. triangularis (caput longum), e.g. 5·5 cm.

Along its whole width it is closely united with fibres of the labral platysma which lie superficial to it. It was impossible to separate the fibres of the labral platysma from those of the M. quadratus labii inferioris.

### Musculus quadratus labii superioris

The combined heads of this muscle together with fibres from M. zygomaticus and M. malaris form a sheet, traceable down to the red lip margin and completely hiding from view the pars peripheralis M. orbicularis oris. The thickness (macroscopic dissection) is about 0·1 cm. half-way between the rima oris and the nose. The separate heads are almost hidden from view by the capita of the M. malaris, especially by the caput mediale.

A peculiar superficial muscle bundle was found running inferolaterally to end near the apex modioli, and composed of fibres derived from the caput infraorbitale. The direction of its fibres is at an angle of about 60° to the muscle fibres (see fig. 1). The two medial heads of the M. quadratus labii superioris (i.e. capita angulare et infraorbitale) form with the pars transversa M. nasalis, a continuous fan-like sheet of muscle.

*Caput angulare.* The most medial fibres of this head form a continuous sheet with the fibres of the pars transversa M. nasalis, and are only artificially separable. The lateral fibres at first sight appeared to form a continuous sheet with the caput infraorbitale but on closer dissection, an oblique line of natural cleavage was found, which indicated that these two heads overlapped to an extent of about 2 mm. Thus these two heads (capita angulare et infraorbitale) have a continuous area of origin, from the os nasale to the infraorbital margin, 5·82 cm. in length (base line).

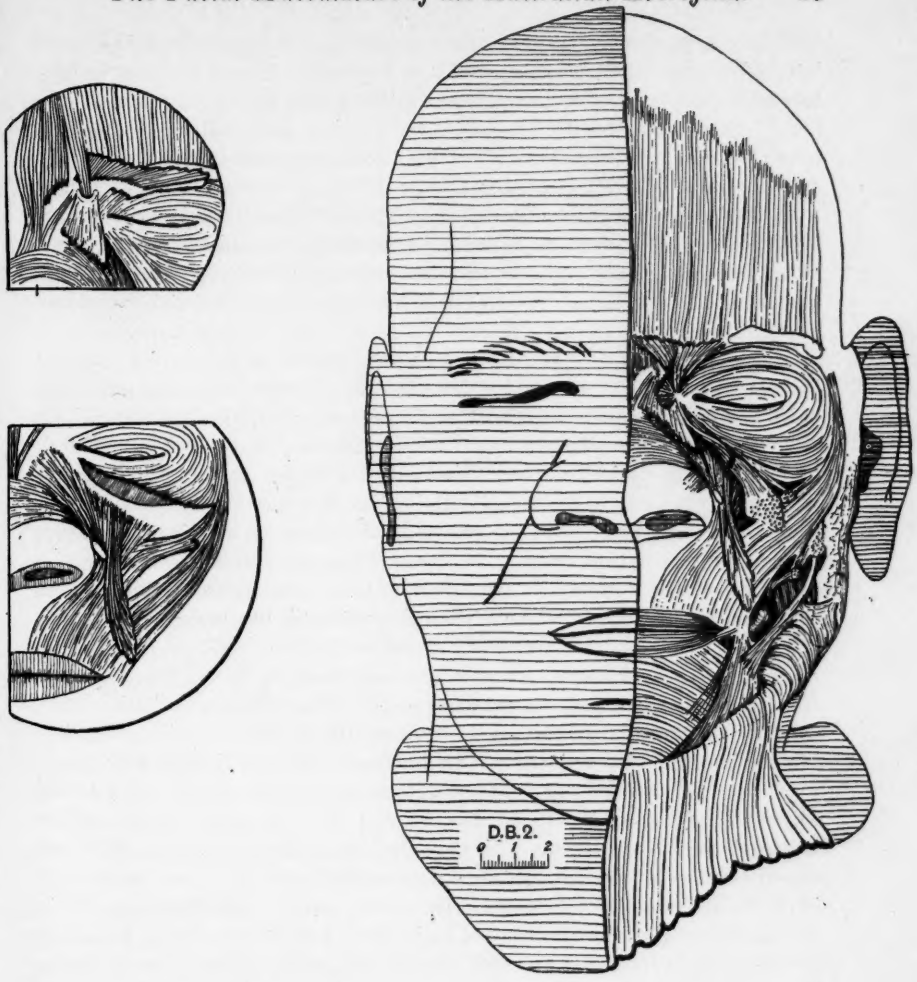


Fig. 1. Norma facialis of D. B. 2 to show the superficial facial musculature. The white oval lateral to the left ala nasi represents the attachment to the skin of the caput angulare M. quadratus labii superioris. The dots inside circles indicate the position of the lower margin of the orbit and the centre of the external auditory meatus respectively. The "moveable torus" is indicated in the eyebrow.

The upper inset shows details of the insertion of the M. procerus and the origin of the caput mediale M. malaris.

The lower inset shows the relationship of the various heads of the M. quadratus labii superioris to each other and of the whole muscle to the pars transversa M. nasalis.

The origin of the caput angulare commences medially from the lower lateral border of the os nasale, within a few millimetres of the middle line; thence it steeply ascends to the level of the medial canthus (1·22 cm.) or a little higher on the frontal process of the maxilla, and finally descends in a curve following approximately the orbital margin for 2·49 cm.

*M. quadratus labii superioris.*

*Insertion.* A few medial fibres are inserted into the ala nasi. Many superficial fibres are inserted into the skin of the naso-labial furrow, at its upper nasal end, for a distance of 1·44 cm. A few fibres, deep to these latter, sweep round the ala nasi, to gain the upper lip and help to conceal the M. orbicularis oris from view.

*Caput infraorbitale.* The origin measures 2·5 cm. in length and 1·90 cm. in breadth, and completely hides the infraorbital foramen from view. The thickness of the muscle is 0·5 cm. near its origin. Laterally it is joined by a narrow but well-defined caput zygomaticum. The combined caput infraorbitale and caput zygomaticum stream down into the upper lip, completely hiding from view the underlying M. orbicularis oris. A few of the most medial and superficial fibres of this caput stream downwards and laterally, crossing obliquely the main fibre sheet of this caput. These fibres lie in the lower portion of the naso-labial furrow and are almost in a direct line with the fibres of the caput angulare which enter the cranial portion of the naso-labial furrow. They reach the apex modioli, and cross superficial to the labial fibres of the caput laterale M. malaris, and of the M. zygomaticus. The greatest width of this band is at the lateral margin of the caput infraorbitale where it is 0·5 cm. in width and 0·1 cm. in thickness. A somewhat similar band is figured in a Melanesian head (No. 221, fig. 25) by L. Harslem-Riemschneider.

*Caput zygomaticum.* This has an origin apparently in common with the M. zygomaticus, and towards its insertion splits into two layers, a thin superficial and a depeer layer, between which lie the facial vein. The most superficial fibres were intimately bound with fibres of the caput laterale M. malaris, and ended with them in the panniculus adiposus of the naso-labial gyrus. The deeper fibres formed the main bulk of the muscle, which joined the lateral fibres of the caput infraorbitale, and ended with them in the upper lip. The deeper fibres formed a well-defined bundle, oval in section. The greatest width was 0·5 cm. and thickness 0·2 cm. Its approximate length, from origin (medial end) to its junction with the caput infraorbitale, is 2·6 cm.

### Musculus zygomaticus

At its origin the muscle is completely separable from the caput laterale M. malaris, which does not quite cover it. On tracing the caput laterale M. malaris towards the modiolus, it blends inseparably with the superficial portion of the M. zygomaticus, and these fused muscles spread out fanwise to their insertion near to which they measure 2·43 cm. in breadth. The M. zygomaticus is inserted into the modiolus (q.v.). The greatest width of the muscle

near the rima oris is 3·43 cm., and the total length of the muscle from the highest point of origin to the apex modioli is 6·0 cm. A small fleshy band separates from the lower border of the M. zygomaticus to end in the panniculus adiposus of the cheek.

The conjoined M. zygomaticus and caput zygomaticum have a large elliptical origin. The greatest length of this origin is horizontal, and measures 2·74 cm.; the greatest width is 0·54 cm. almost at its anterior end, being immediately posterior to the caput zygomaticum fibres. The lower margin of this origin runs almost parallel with the upper margin of the masseter muscle tendon, and approximately 0·4 cm. above it.

*Musculus caninus.* This is a broad sheet of muscle, somewhat concave owing to the concavity of the infraorbital fossa, from which it takes origin. Its origin lies not transversely as in H. B. 1 but is more or less U-shaped, with two large horns, medial and lateral. The width from the tip of one horn to that of the other is 3·1 cm. The lateral horn extends inferolateral to the infraorbital foramen, from which it lies 0·8 cm. distant.

The upper part of the medial horn has a separate origin from the frontal process of the maxilla, immediately below the orbital origin of the caput angulare M. quadratus labii superioris (cf. fig. 5). It extends to within 1·5 cm. of the internal canthus.

Some of these fibres are attached to bone inferiorly (2·3–2·4 cm. below its upper end) and therefore form a true M. anomalus maxillae; the remainder of these fibres continue into the main mass of the M. caninus.

The position and direction of the medial horn corresponds to the vertically directed bundles seen in the M. anomalus maxillae in H. B. 1 and European heads. This fact is of interest inasmuch as hitherto the M. anomalus maxillae has been considered chiefly as a derivative of the pars transversa M. nasalis.

The central fibres of origin are 1·38 cm. below the infraorbital foramen. The width just above the point where it passes through the fibres of the M. zygomaticus is 1·08 cm. and the thickness at this point is 0·20 cm.

The medial border of the muscle is in close apposition to the M. incisivus superioris below and the pars transversa M. nasalis above. The origin of the M. incisivus is separated by 1 or 2 mm. from the most medial fibres of the M. caninus.

*Musculus triangularis.* There is a well-marked caput longum which has a well-developed lateral extension, attached to bone. This extension takes the place of the caput latum. It will be remembered that the caput longum was differentiated from the caput latum by the fact that its fibres arose from bone, whereas the fibres of the caput latum took origin from fascia and had no attachment to bone. The distance from the mid-line to the distal edge of the lateral extension near the lower border of the mandible is 5·5 cm. (The muscle is 4·0 cm. broad along the same line, and the origin of the distal edge is 0·6 cm. above the lower border of the mandible, measured at right angles to the lower border. Medially, the origin is at the lower border of the mandible,

where the M. quadratus labii inferioris, and pars mandibularis platysmae have a common point of attachment below the tuberculum mentale.

The width of the M. triangularis, just before it enters the modiolus, is 1·7 cm.

A small caput transversum is present. The caput buccale is well developed and has a strong tendinous origin from the panniculus adiposus covering the tendon of the masseter. Its fibres curve downwards and forwards slightly inferior to the apex modioli and lie superficial to the lateral fibres of the caput longum.

A "muscle triangulare interne" (Cruveilhier), which was counted as part of the caput latum, was present, being represented by a few fibres (fig. 2).

*Caput longum.* The muscle was typically triangular in shape. Its most medial fibres form a well-marked band arising from the region of the tuber mentale, and proceed obliquely upwards to end in the modiolus. The more lateral fibres arise from a series of oblique lines on the mandible, which interdigitate with the obliquely running fibres of the pars labralis platysmae. The lateral fibres of the caput longum thus form a series of short arches over the separate bundles of the labral platysma, whereas the medial fibres of the caput longum form one large arch or loop over the whole of the labral platysma.

*Musculus orbicularis oris.* The pars peripheralis was large and well developed, and dark red in colour. It was completely covered in the upper lip by the labial tractors and fibres from the M. zygomaticus, and in the lower lip by the inferior labial tractors, with the exception of a small area near the angle of the mouth. The pars marginalis, in both upper and lower lips, had the typical twist, as the fibres were traced to the angle of the mouth (cf. Part I).

A well-developed pars nasalis is present, partly hiding the fibres of the pars alaris M. nasi, and inserting in part into the medial vestibular cushion.

The width (in the middle line) of the inferior part of the muscle from the rima oris is 2·66 cm., and its lower edge lies a little inferior to the sulcus mento-labialis. The width of the upper part from nose to rima oris is 2·79 cm. (in the middle line).

### The Modiolus

*Description of the insertion of the muscles taking part in the formation of the modiolus, with an accompanying figure (fig. 3)*

The most superficial muscle at the apex modioli is the abnormal slip of the caput infraorbitale M. quadratus labii superioris which has already been described. This lay superficial to the superficial fibres of the M. zygomaticus. The numbers in fig. 3 are the same as those given to the muscles below.

(1) *M. zygomaticus* is formed of two portions, superficial and deep, separated by the M. caninus, as is usually the case. The superficial portion enters the apex modioli, immediately beneath the fibres above mentioned. The fibres are closely bound with the underlying M. caninus.

As in H. B. 1, the superficial lateral and medial portions formed the superficial portion of the modiolar insertion. The most medial fibres of the muscle did not enter into the formation of the modiolus, but passed medial

Fig. 2. Norma lateralis of D. B. 2 to show the superficial facial musculature. The conventions are the same as on fig. 1.

to this to cover the pars peripheralis M. orbicularis oris, thus contributing fibres to the superior labial tractor.

Some of the superficial fibres ran into the M. triangularis and portio modiolaris platysmae.

The deep portion (composed of the deep lateral fibres only) has a large and continuous insertion into the basis modioli including the superior cornu (cf. fig. 3). It is separated by cellular connective tissue from the M. caninus.

(2) *M. incisivus superioris.* This has a superficial and a deep insertion. The superficial enters the apex modioli on the same level as the superficial portion of the M. zygomaticus, with whose fibres it is closely interlaced.

The deep fibres are inserted into the superior cornu of the basis modioli (cf. fig. 3).

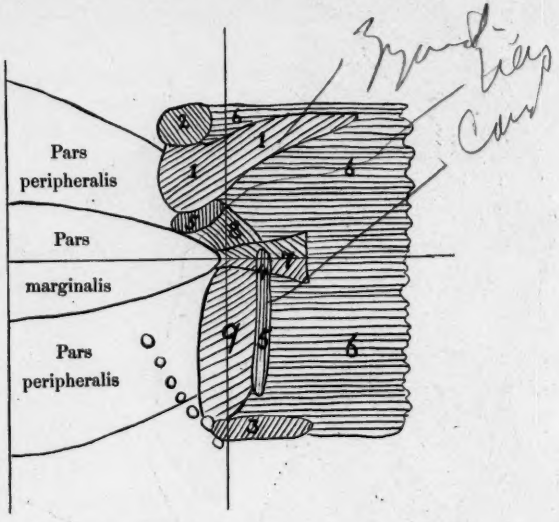


Fig. 3. A diagram of the basis modioli showing the attachments of the various muscles.

1. M. zygomaticus.
2. M. incisivus superior.
3. M. incisivus inferior.
4. M. caninus.
5. M. triangularis.
6. M. buccinator.
7. Pars marginalis M. orbicularis oris.
8. Pars peripheralis superior M. orbicularis oris.
9. Pars peripheralis inferior M. orbicularis oris.

(3) *M. incisivus inferioris.* There seems to have been no superficial attachment of this muscle to the modiolus in D. B. 2, all its fibres entering the inferior cornu and basis modioli.

(4) *M. caninus.* These fibres enter the modiolus by passing betweeen the two heads of the M. zygomaticus. The majority of the fibres are continued on into the M. triangularis, from which they are inseparable. In the cellular tissue which separates the M. caninus from the deep insertion of the M. zygomaticus, lay the external maxillary artery.

(5) *M. triangularis.* This consists chiefly of the caput longum and caput

buccale. With the caput longum will be included the caput transversum and a few internal fibres of the caput latum (muscle triangulare interne). A large proportion of the fibres form a caninus-triangularis complex, which forms a large mass in the region of the apex modioli. The most lateral and deep fibres of the caput longum pass upwards to be inserted into the superior cornu of the basis modioli.

A large number of the other deeper fibres are inserted into the basis modioli along an area common to it and the M. caninus. For the most part the M. caninus occupies the upper half, and the M. triangularis the lower half of this area.

The caput buccale fibres enter below the apex modioli, and in so doing cross the posterior margin of the caput longum fibres.

(6) *M. buccinator.* This has a very large insertion into the basis modioli. As will be seen in the diagram many of the maxillary fibres are inserted above the deep portion of the M. zygomaticus, though lateral to the deep portion of the M. incisivus superior.

(7, 8, 9) *M. orbicularis oris.* Pars marginalis superior and inferior. The pars marginalis superior fibres all passed deep to the pars peripheralis at the angle of the mouth, to gain a common axial insertion into the basis modioli with the pars marginalis inferior. The pars marginalis inferior has superficial fibres passing to a superficial area between the apex modioli and the angle of the mouth. These fibres come mainly from the lower superficial surface of the pars marginalis inferior. The remainder of the fibres curl round the pars peripheralis to be inserted into the basis modioli as described above.

(8, 9) Pars peripheralis superior and inferior. These two muscles are inserted into the whole thickness of the modiolar mass from apex to basis.

*The dimensions of the modiolus.* The measurements are taken from horizontal and vertical lines drawn through the angles of the mouth.

| | | |
|---|---|---|
| (1) | Thickness ... ... ... ... ... | approx. 1 cm. |
| (2) | Distance of apex from angle of mouth ... | ,, 1 cm. |
| (3) | Sup. cornu, greatest breadth medial to vertical line ... | 0·73 cm. |
| (4) | Greatest height of basis modioli above horizontal line... | 1·65 cm. |
| (5) | Inf. cornu. This is practically absent, the M. incisivus inferior insertion lying in the vertical line | |
| (6) | The greatest depth of basis modioli below the horizontal line ... ... ... ... ... ... ... | 2·0 cm. |

### Musculus incisivus superioris

This muscle is well developed. Some of the lateral fibres interlace with, and have a common origin with those of the pars transversa M. nasalis, while others continue into it. Others interlace with the pars alaris M. nasi, and the most medial fibres are continuous with those fibres of the M. orbicularis oris which extend up on to the septum.

*Musculus mentalis.* The M. mentalis was powerful and well developed, and had the typical arrangement, with the medial fibres forming a series of loops, and the more lateral fibres passing to the skin.

A M. anomalus menti was present, its fibres lying inferolateral to the main body of the M. mentalis. These form a well-marked, fan-shaped sheet of pale fibres, directed vertically. It forms a continuous sheet of fibres with the M. praemandibularis transversus. The total width of this muscle sheet is 3·0 cm., and its medial edge is distant 1·5 cm. from the middle line. The origin of the M. mentalis is 1·0 cm. wide and 0·85 cm. in height and extends on to the canine jugum.

Its lower border is 1·55 cm. from the inferior border of the mandible.

The typical fibrous pad, with a well-developed bursa beneath it, was present. No definite fatty pad could be distinguished between this and the mucous membrane such as is described by Virchow.

### Musculus incisivus inferioris

This was powerful and well developed, and has the usual origin lateral to the M. mentalis and from there its fibres spread out in the form of a fan. The superior fibres go to the modiolus, a few intermediate fibres pass into the platysma, and the lowermost fibres pass to bone, forming a broad, very thin, pale sheet, passing immediately inferior to the mental foramen (= M. praemandibularis transversus, Eisler). The combined M. praemandibularis transversus and M. anomalus menti form a thin muscular sheet which covers the lower part of the anterior surface of the corpus mandibulae, reaching laterally as far as 0·8 cm. beyond the mental foramen (lateral edge).

The origin of the M. incisivus inferioris lay immediately lateral to the canine jugum alveolare, and was 0·7 cm. in depth.

### Musculus orbicularis oculi

#### Pars peripheralis (M. malaris)

This is very well developed and the usual two heads could be distinguished.

*Caput laterale.* This is a well-marked sheet, continuous with and inseparable from the lateral border of the pars orbitalis. It extends a little more than 1·0 cm. above the line joining the ectocanthion to the external auditory meatus. Laterally and superiorly it interlaces with and lies superficial to a well-developed M. orbito-auricularis. Laterally it does not completely overlap the M. zygomaticus. Towards its insertion it joins inseparably with the M. zygomaticus and gives off various small bundles to end in the panniculus adiposus. Here it is partly crossed superficially by the fibres of the M. oculo-buccalis (caput mediale).

*Caput mediale.* For convenience of description this caput has been divided into two portions, a nasal (medial) and an ocular (lateral) which in this subject appear to be separated at their origin by the angular vessels, but a

little lower down, they unite, concealing the vessels. The ocular or lateral portion (M. oculo-buccalis) is well developed, though not as powerful as in H. B. 1.

It measures 5 cm. in length, its width is 0·53 cm., and its thickness is 0·4 cm. It forms a thickened inferomedial margin to the pars orbitalis, and ends in the panniculus adiposus of the cheek, crossing and lying superficial to the caput laterale. Its most lateral or ocular fibres are intimately interlaced with the lowest fibres of the pars orbitalis and cannot be separated from them. It is these fibres which end in the cheek. The insertion into the cheek is 5 cm. from the mid-line, and approx. at the level of the lower border of the ala nasi, and 3·58 cm. from the angle of the mouth.

The fibres are similar in size and colouring to the pars orbitalis.

The nasal or medial portion is an irregular sheet.

The main bulk of its fibres end laterally in the skin of the bridge of the nose, and the inferior margin of the upper pole of the naso-buccal gyrus where they are inserted "en echelon." The whole mass lies superficial to the caput angulare of the M. quadratus labii superioris. The origin of the nasal portion of the caput mediale (cf. fig. 1 *a*) is from a fibrous loop which encloses the bony insertion of the M. frontalis (cf. M. frontalis). The medial limb of this loop takes origin from bone in the region of the pseudonasion immediately lateral to the bony origin of the M. procerus (q.v.). The lateral limb arises from bone immediately above the medial canthus.

The pars orbitalis and pars palpebralis were well developed, but do not warrant a separate description.

A movable fibro-muscular torus was present immediately lateral to the bony torus, similar to but containing more muscular fibres than in H. B. 1. These muscle fibres were derived from the surrounding muscles, more especially from the M. depressor capitis supercilii.

The following measurements were taken. (N.B. In these measurements the word pupil is used to describe a point midway between the endo- and ectocanthion.)

| | |
|---|---|
| Pupil to upper margin of muscle ... ... ... | 2·2 cm. |
| Maximum height of upper part of muscle ... | 2·5 „ |
| Pupil to lateral margin (including M. malaris) ... | 5·3 „ |
| Ectocanthion to lateral margin ... ... ... | 4·0 „ |
| Bony orbital margin to lateral margin of muscle | 3·0 „ |
| Pupil to inferior margin ... ... ... ... | 2·35 „ |
| Pupil to medial margin ... ... ... ... | 2·1 „ |
| Endocanthion to medial margin ... ... ... | 0·65 „ |
| Pupil to ectocanthion ... ... ... ... | 1·5 „ |
| Endo- to ectocanthion ... ... ... ... | 2·8 „ |

### Musculus depressor capitis supercilii

This is a well-developed muscle. It consisted of a superficial and a deep set of fibres. The main body of the superficial fibres formed the most lateral part of the muscle at its insertion into the brow. A few of these superficial fibres ran almost horizontally and medially to form a small fan which lay superficial to the origin of the caput mediale M. malaris, where they ended in the panniculus. These fibres at first seemed to be continuous with the caput mediale M. malaris. The origin of the superficial fibres is more or less vertical, from bone, and extends as low as the medial palpebral ligament from which they also arise. It twists from this vertical origin into a horizontal transverse insertion. The deep fibres formed the most medial portion of the muscle at its insertion into the brow. These fibres passed laterally beneath the superficial fibres, to arise from bone a little above and medial to the superficial fibres, and directly continuous with the lowermost origin of the upper part of the pars orbitalis M. orbicularis oculi.

At its insertion medially it reaches to the middle line (i.e. to the glabellar region) and partly conceals the M. depressor glabellae or procerus. Laterally the superficial portion runs into the fibro-muscular pad or movable torus of the eybrow. From its insertion into the glabella to its insertion into the movable torus it measures 2·85 cm. The origin of the superficial fibres measures 0·6 cm.

### Musculus corrugator supercilii

This muscle was exceptionally well developed. The origin was very extensive; medially it is 0·65 cm. from the middle line, and it extends laterally to a distance of 2·35 cm. from the middle line but does not reach the supraorbital notch. The total width of the muscle is 2·1 cm.

The origin medially is below the torus, and extends laterally with a sinuous outline, and comes to lie almost within the orbit, so that the lateral fibres are directed almost horizontally forward, while the medial fibres are inclined a little more vertically (cf. fig. 1 *a*).

The origin does not reach the supraorbital notch, which was abnormally lateral in position. The lateral fibres of the muscle gradually crossed the notch, as they streamed out into the tail of the eybrow, and the fibrous torus. The length of the medial fibres was 1·68 cm. The origin is musculo-tendinous. Its insertion lies beneath the eybrow, and passes into the whole thickness of the eyebrow region from the skin down to and probably including the middle layer of the galea (cf. Eisler and fig. 4). Here it interlaces with the M. frontalis, M. orbicularis oculi, and M. depressor capitis supercilii.

Its insertion extends from the head of the eybrow almost to the lateral limit of the movable torus, and runs immediately posterior to the torus, in which many of its fibres ultimately end. Lateral to the muscle was seen a well-marked pad of fat described by Charpy "poussinet adipeuse" (see Whitnall), but no trace of it was seen where the muscle was present.

### Musculus procerus

This muscle forms a broad sheet, continuous above with the M. frontalis, and augmented laterally by some small bundles which lie lateral to the caput mediale M. malaris. Followed downwards, the muscle narrows to a thick sheet, a large percentage of whose fibres on the left side are inserted into the periosteum:

(*a*) of the nasal bone in the region of the pseudo-rhinion.

(*b*) A few fibres extend downwards to interlace with the pars transversa M. nasalis.

(*c*) An accessory bundle of fibres arises close to the origin of the caput mediale M. malaris and runs obliquely downwards towards the middle line, to join with those fibres of the M. procerus which gain the pars transversa M. nasalis.

On the right side, the muscle is again broad just below the glabella and continuous with the sheet of the left side. This sheet interlaces laterally with fibres of the right M. depressor capitis supercilii. Below it narrows and thickens to be inserted in part into the periosteum of the os nasale below the pseudo-rhinion. Some fibres, however, pass on to interlace with the fibres of the pars transversa, and here the muscle widens a little below the pseudo-rhinion, so that on this side we see the hour-glass shape which was not present on the left side.

### Musculus frontalis

This is a well-developed sheet, extending back from the glabella for 8·4 cm., and from the supraorbital margin laterally for 9 cm.

Medially it is continuous across the middle line with its fellow of the opposite side. Laterally it interlaces with the M. auricularis superior, and with the M. orbito-auricularis. The fibres were coarse and the colour dark.

Medially a few fibres of the muscle continued over the arcus supercilioris to gain attachment to bone near the root of the nose. This attachment is arched over by a fibrous loop of origin of the nasal portion of the caput mediale M. malaris (q.v.). These fibres of the M. frontalis cross superficial to the most medial portion of the M. corrugator supercilii. The approximate width of the M. frontalis is 6·0 cm. from the middle line outwards.

## V. Galea aponeurotica. D. B. 2

Both Eisler and Whitnall are in agreement in describing the galea aponeurotica as splitting into two layers to enclose the M. frontalis anteriorly, but they differ as to the relations of the deeper of these two layers. According to Eisler (pp. 167–8) the under-surface of the muscle is united by tendinous fibres to the deeper layer which he called the "Stirngalea," and which fades away into loose connective tissue in the region of the M. corrugator supercilii, M. depressor capitis supercilii, and M. procerus. According to Whitnall (p. 109) the galea

splits to enclose the M. frontalis, and its deeper layer "is firmly attached to the supraorbital margin."

On examining D. B. 2, the galea was still found to split to enclose the M. frontalis, but on the deep surface of the muscle two distinct layers were

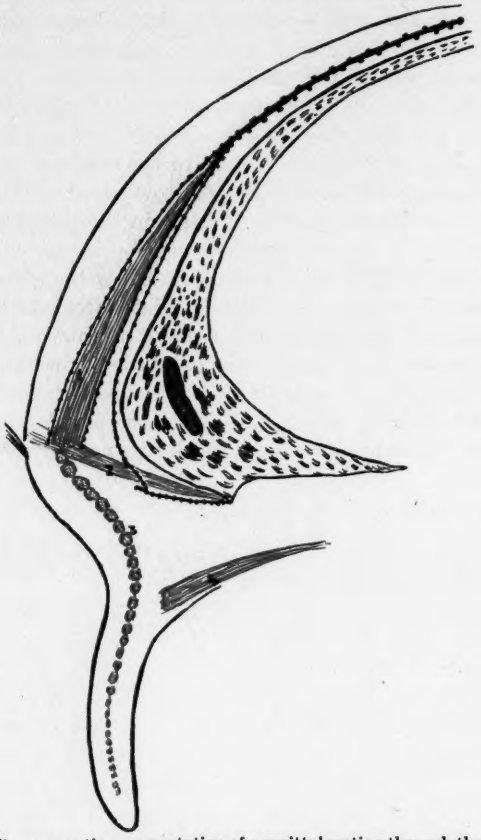

Fig. 4. A diagrammatic representation of a sagittal section through the bony torus about its centre showing the relationships of the three layers of the galea aponeurotica.

1. M. frontalis.
2. M. corrugator supercilii.
3. M. orbicularis oculi.
4. M. levator palpebrae superioris.

found, united by fine connective tissue, but easily separable. The more superficial of these corresponded to the layer described by Eisler, while the deeper conformed to that described by Whitnall. Thus at the junction with the M. frontalis, both superiorly and laterally, the galea aponeurotica splits into

three layers, one running superficial to the M. frontalis, and the other two deep to it. The deepest layer of the galea was easily separable from the periosteum, and at the supraorbital notch, the supraorbital vessels and nerves lay between the periosteum and the deepest layer of the galea (cf. fig. 4).

In other respects the galea was found to be normal, and its bony attachments anteriorly (e.g. root of nose, orbital margin, etc.) were found to agree closely with that already described in H. B. 1.

### Musculus occipitalis

This is a small, poorly developed muscle sheet, 5·3 cm. in total width, its greatest height being 3 cm., and 0·11 cm. thick, while the distance of its inner border from the middle line is 4·0 cm. inferiorly and 5·0 cm. superiorly. Otherwise it has the normal origin and insertion.

### Musculus auricularis posterior

The muscle consists of three portions, two large bellies inferiorly, and a large fan-shaped sheet superiorly.

(*a*) The lower belly arises from the upper part of the mastoid process (immediately above the origin of the anterior portion of the M. sternomastoideus) and measures 3·68 cm. in length, its thickness is 0·18 cm. and its width 0·5 cm. It is inserted into the lower portion of the eminentia conchae by a flat expanded tendon.

(*b*) The second belly is shorter and broader, taking origin from the upper part of the mastoid process, slightly above and anterior (1·0 cm.) to the origin of the lower belly, and 1·74 cm. above the tip of the mastoid process. It runs upwards and forwards to be inserted into the upper part of the eminentia conchae, and is 0·8 cm. in breadth, 0·2 cm. thick, and 2·0 cm. long. Superiorly it is almost inseparable from the lowermost fibres of the following large fan-shaped sheet of muscle.

(*c*) The uppermost fan-shaped sheet of muscle arises partly from the upper part of the mastoid process, and partly from the galea. Superiorly it is continuous with, and inseparable from, the M. auricularis superior. It is partly covered by, and closely interwoven with, the fibres of the M. occipitalis. It is inserted into the uppermost part of the eminentia conchae, in continuity with part (*b*). Its approximate radial length is inferiorly (to the mastoid process) 3·2 cm. and superiorly (to the galea) is 3·7 cm.

### Musculus auricularis anterior and superior

These two muscles were inseparable from one another, were well developed and formed a broad fan-shaped sheet. (This was continuous posteriorly with the upper two portions of the M. auricularis posterior, so that the three muscles formed a practically continuous sheet.) The greatest length of the M. auricularis anterior, from the spina helicis to the M. frontalis, was 6·36 cm. The greatest vertical length of the M. auricularis superior, from the ear-scalp junction

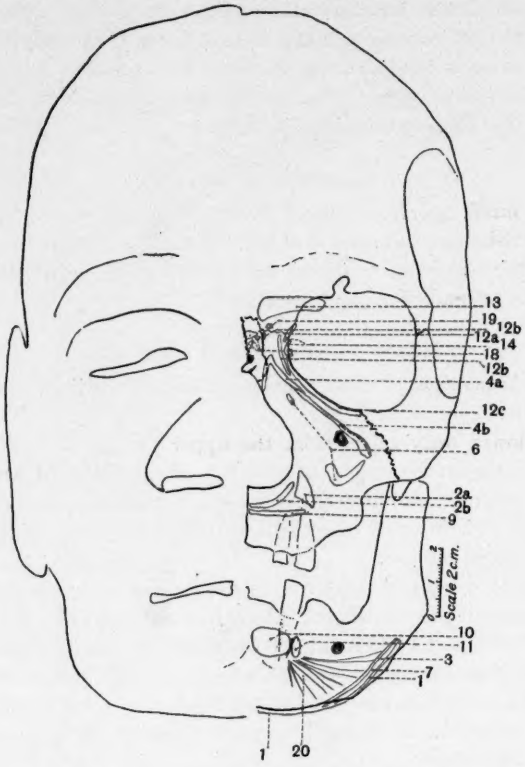


Fig. 5. Norma facialis of left half of the skull of D. B. 2 to show the angles of the various facial muscles. (See also Fig. 6.)

1. Platysma (portio mandibularis).
2 *a*. Pars transversa } M. nasalis.
2 *b*. Pars alaris }
3. M. quadratus labii inferioris.
4 *a*. Caput angulare } M. quadratus labii superioris.
4 *b*. Caput infraorbitale }
4 *c*. Caput zygomaticum }
5. M. zygomaticus.
6. M. caninus.
7. Caput longus M. triangularis.
8. M. buccinator.
9. M. incisivus superioris.
10. M. mentalis
11. M. incisivus inferioris.
12 *a*. Pars orbitalis.
12 *b*. Pars oculobuccalis.
12 *c*. Nasal.
13. M. corrugator supercilii.
14. M. depressor capitis supercilii.
16. M. occipitalis.
17. M. auricularis posterior.
18. M. procerus.
19. M. frontalis.
20. M. anomalus menti and praemandibularis transversus.

upwards is 4·6 cm. The insertions of the two muscles were also continuous. The M. auricularis anterior lay wholly superior to the ramus frontalis of the M. temporalis superficialis, while the two muscles covered a large portion of the ramus parietalis, and the point of bifurcation of the two rami of the artery.

*M. transversus nuchae* and pars nuchalis of the M. auriculo-occipitalis (Ruge). In Spalteholz' *Atlas* (vol. II, 11th German ed., fig. 354) the space between the uppermost origins of the M. trapezius and the M. sternomastoideus is shown bridged by a curved strong band of fibrous tissue. In D. B. 2 this band was composed chiefly of muscle fibres, and represented the pars nuchalis

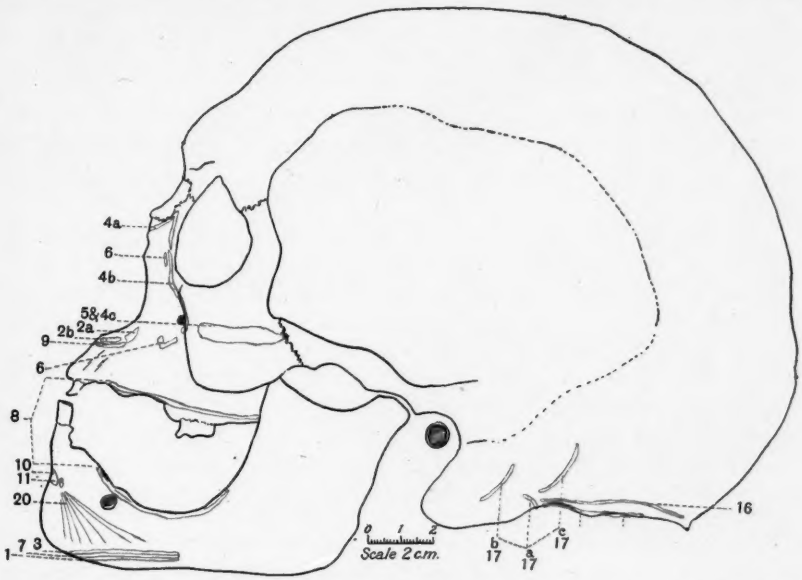


Fig. 6. Norma lateralis of the skull of D. B. 2 to show the origins of the various facial muscles. For numbering see fig. 5.

M. auriculo-occipitalis of Ruge (M. cervico-auriculo-occipitalis of Huber). From it took origin the most anterior fibres of the M. trapezius which were separated superiorly from the main body of the muscle. Deep to this, a large and well-developed M. transversus nuchae filled in the whole of the crescent-shaped gap, up to the nuchal line. The M. semispinalis capitis was completely hidden. The length of the M. transversus nuchae was 2·8 cm. and the breadth was 1·3 cm.

A few skin muscle fibres crossed the mastoid process transversely, connecting these muscle bands with the bellies of the M. auricularis posterior.

Therefore in this subject there are present "reste" of the two layers of the platysma met with in some anthropoids and some mammals (e.g. dog):

(*a*) the crescent-shaped remains of the superficial layer of the platysma, viz. the pars nuchalis M. auriculo-occipitalis (Ruge), and (*b*) the remains of the deep layer of the platysma, namely the M. transversus nuchae, lying deep to the above.

The few thin muscle fibres seen passing across the mastoid process probably belong to this deeper layer, and thus really form part of the M. transversus nuchae. Fig. 2 shows the conditions met with.

### Musculus auriculo-orbitalis

This forms a relatively well-developed, though irregular, fibro-muscular sheet, lying wholly inferior to the ramus frontalis of the A. temporalis superficialis. Anteriorly the relationship of its fibres from above downwards are threefold.

(*a*) They interlace with lateral fibres of the M. frontalis.

(*b*) Below this they are covered partly by the M. malaris of M. orbicularis oculi, and passing beneath this interlace with the pars orbitalis, while still lower

(*c*) they are attached beneath the M. orbicularis oculi to fascia covering the lateral bony margin of the orbit. Superiorly the muscle has a well-marked curved fibrous margin, though a weak sheet of muscle fibres lay still higher between this margin and the ramus frontalis A. temporalis superficialis (cf. fig. 2). Inferiorly two thin slips extended down over the zygomatic arch and the facial nerve respectively to end in the thick fascia close to the parotid gland. Posteriorly, the fibre crossed superficial to the A. temporalis superficialis and ended irregularly in fascia. The length of the upper crescentic border was 6·6 cm. The length of the lower crescentic border was 5·9 cm. The width (vertically) immediately lateral to the M. malaris was 2·7 cm. The thickness was approximately 0·18 cm.

## GENERAL DISCUSSION AND RACIAL COMPARISON

In the two Australian aboriginal heads dissected, the following general features are to be observed:

When compared with the European, the muscle bundles are exceedingly coarse, as seen with the naked eye; they also appear much darker red than in the European head. The muscles are also much thicker and more powerful and show much more extensive areas of origin. There is also much less apparent differentiation between the muscles, especially in the mid-facial region.

This lack of differentiation in the mid-facial region is due partly to the increased size of the muscles usually described in this region, but chiefly to the more massive development of a superficial sheet, which we have termed the M. malaris (pars peripheralis M. orbicularis oculi) and which was originally described by Henle in the European face.

A further expression of this apparent lack of differentiation, which may be simply due to enlargement and consequent approximation of the various muscles, is to be seen when we examine the bony origins.

From the figures it will be seen that the origin of the M. caninus, M. nasalis, and M. incisivus superioris are practically continuous, and also it may be remarked, very extensive.

A similar condition is seen in the origins of the three heads of the M. quadratus labii superioris.

The data for these latter comparisons is wholly based on the anatomical text-books, which are based upon the condition in the European.

The wide and powerful development of this M. malaris sheet completely conceals from view the underlying muscles, e.g. the M. quadratus labii superioris, and must be held to be largely responsible for the observations of various authors that this mid-facial region shows a lack of differentiation in many non-European races (Chinese, Hottentot, Herero, Japanese and Chinese, Papuan).

A further and peculiar feature of this M. malaris is the well-marked development of a portion of its inner head to form a strong muscle in the naso-buccal gyrus ("M. oculo-buccalis"). This muscle always seems to end in the superficial fat of the cheek and to lie anterior to the other muscles of the mid-facial region.

Further, the labial tractor muscles (M. quadratus labii superioris, M. quadratus labii inferioris and pars labralis platysmae, together with the labial fibres of the M. zygomasticus) are especially well developed, in so far as they form a thick muscular sheet covering the lips, right up to the red line. In the upper lip especially this sheet, to which the M. zygomaticus contributes, is very much more marked than in the European.

Finally, the presence in the outer part of the eyebrow region, of a movable torus, which in one head was mainly fibrous, and in the other was fibro-muscular, would seem to be a feature of the aboriginal.

## RACIAL COMPARISONS DETAILED

### Racial Comparison of Muscle Groups

*Platysma myoides.* The development of the platysma in these two aboriginal heads is variable, and in both cases they resemble Type III of Bluntschli. No further opinion can be expressed as to whether this is the prevailing type, but there was no tendency towards a horizontal direction of the fibres. The weak, poorly developed condition of the neck portion of the platysma in H. B. 1 may be only an individual peculiarity, but certainly formed a marked contrast to the remainder of the platysma, which was very coarse and powerfully developed. As regards the Japanese and Chinese, Kudo says that he had not as yet been able to discover any apparent difference between the Japanese, Chinese and European types. In two Sunda Island heads (Javanese)

Koster found a well-developed neck and nape platysma to be present and a well-marked pars aberrans ascendens of the neck platysma, in both cases. These two heads showed much greater complexity than that seen in the two Australian aboriginal heads.

In fourteen Papuan and Melanesian heads, L. Harslem-Reimschneider found the muscle to vary greatly both in the development and in the presence or absence of the pars aberrans. Zeidler found the nape platysma to be absent in five adult Herero heads, and in three Herero and Hottentot children's heads practically no pars aberrans was present. Fetzer found in seventeen Hottentot heads that there was no nape platysma, though von Eggeling found it present eight times in six Herero and Hottentot heads. The pars aberrans was poorly developed in six heads, and well developed in one head.

From the above, it is clear that from the platysma, very little information is to be obtained concerning racial differences. Though it is extremely variable, the presence of a pars aberrans seems to be more frequent in higher racial types; in neither of the aboriginal heads examined by us was it present.

*Musculi nasi.* Only in one of these heads were all these muscles well developed. The pars alaris could not be separated from the pars transversa. A perusal of the literature seemed to indicate that very little information with regard to racial comparisons could be obtained from these muscles. Kudo states that "size and shape of the nose are no criteria for the development of the pars transversa M. nasalis."

*Musculi quadrati labii.* These muscles extended over and concealed the M. orbicularis oris up to the red margin of the lip, in a manner much more marked than in the European. The M. quadratus labii inferioris showed no difference other than size. In the case of the M. quadratus labii superioris the origins of the heads were much more extensive, and tended to overlap. The caput angulare and caput infraorbitale overlapped for some distance, and were only differentiated by a definite plane of cleavage.

Only near its origin was the caput zygomaticum differentiated from the infraorbital head, and here its fibres were more or less continuous with that of the M. zygomaticus.

In both cases some fibres from the M. malaris joined the caput zygomaticum.

In the Chinese and Japanese, Kudo figures a similar condition.

The differentiation of the capita described by Koster in the Sunda Islander was not encountered in the Australian aboriginal.

In the Herero head Zeidler found conditions which closely resembled those observed by us.

In the Hottentot also, Fetzer found the same powerful development and lack of differentiation.

In the Papuan and Melanesian, as dissected by L. Harslem-Riemschneider, a much greater variability was present, some approaching the Australian aboriginal, while others approached the Europeans in the respective lack or presence of differentiation.

(1) *Musculi cruciati.*

(*a*) *M. zygomaticus.* In both heads, the M. zygomaticus was very powerfully developed, and its superficial fibres completely overlapped and concealed the lateral portion of the M. orbicularis oris of the upper lip. In each case its origin was almost concealed by the caput laterale M. malaris. The fibres of the latter muscle fused with the bellies of the caput zygomaticum and M. zygomaticus in each case. The splitting of the insertion of the M. zygomaticus, by the M. caninus, was found in both cases, as in the European. Kudo's observations show that the muscle was not so extensively developed in the Japanese and Chinese as in the Australian aboriginal.

In the Sunda Islander, Koster found the muscle well developed but not extending beyond the naso-labial furrow.

L. Harslem-Riemschneider seldom describes any bony origin for this muscle in Papuans. In a few heads a partial extension over the M. orbicularis oris is figured, but only in figs. 18 and 19 does this approach the condition seen in the Australian aboriginal. In some heads the caput zygomaticum and M. zygomaticus were inseparable throughout their length. This condition was not found in either of the aboriginal heads.

Zeidler found that in the Herero the muscle was larger than in the European.

In the Hottentot head, Fetzer found a close relationship with the M. quadratus labii superioris and with the M. orbicularis oculi (lateral fibres).

(*b*) *M. triangularis.* This muscle will not be treated as a whole, but the caput longum and latum will be treated together, representing as they do approximately the M. triangularis of other observers.

The caput buccale, representing the M. risorius of Santorini, and the caput transversum, representing the M. transversus menti, will be separately discussed. The "M. triangulaire interne" will be discussed with the caput latum.

In both heads the caput longum was powerfully developed, and in both the caput latum was poorly developed, although in each case there was a well-marked "M. triangulaire interne." The bony origin in H. B. 1 did not extend lateral to the tuber mentale, while in D. B. 2 it extended as far as the coronal plane of the first molar tooth. The caput buccale was present in both heads, being poorly developed in H. B. 1 and moderately developed in D. B. 2.

The caput transversum was found in both heads, though feeble in H. B. 1. Owing to the difficulties encountered in the dissection of the head of H. B. 1, an interpretation more liberal than that of previous authors may have been applied to the term "caput transversum" (M. transversus menti). No fibres that had attachment to the protuberantia mentalis between the two tubercula mentales were considered as part of this muscle.

Kudo thought that the M. triangularis (caput latum and longum) was better developed in the Mongolian than in the European, while the caput

transversum (M. transversus menti) was constantly found in the Mongolian. Kudo found that the M. risorius was better developed and less often absent in the Mongolian head. Koster found the muscle to be well developed, with a well-marked M. risorius and M. transversus menti in the heads of two Sunda Islanders. The bony origin varied very similarly to that found in our aboriginal heads.

L. Harslem-Riemschneider found in the Papuan and Melanesian head, that the muscle was powerfully developed; the M. risorius was variable and often absent, and in one or two cases a "M. triangulaire interne" was present. The M. transversus menti was usually present.

Zeidler found that the muscle was well marked and more developed in the Herero than in the European. The M. transversus menti was rare, and the "M. triangulaire interne" was never observed.

The M. risorius was variable, being sometimes present, sometimes absent, but in general was more frequent in the Herero than in the Hottentot.

Fetzer confirms Zeidler's observations, and found that the M. risorius was very infrequent in the Hottentot. The M. triangularis was well developed though no "M. triangulaire interne" was found. The M. transversus menti was present in all but one case.

(2) *Musculi transversi.*

*M. orbicularis oris.* Except for its increase in size, this muscle was similar to that of the European.

In D. B. 2, as in the European, the whole of the pars marginalis of the upper lip curls laterally around the pars peripheralis, while in H. B. 1 only a portion of the fibres of the pars marginalis pursue this course, the remainder remaining parallel with the fibres of the pars peripheralis. This may be a more primitive condition.

With regard to these muscles, Kudo found no difference in the Mongolians from the Europeans, and Koster observed no special peculiarities in the Sunda Islander.

L. Harslem-Riemschneider again observed no special peculiarities, in the Papuan and Melanesian, though circular fibres were observed and a pars nasalis was present.

Zeidler found that the muscle was well developed in the Herero and Hottentot, and found some circular fibres, as well as a pars nasalis.

Fetzer found no peculiarities in the Hottentot.

*M. incisivi.* These muscles were powerfully developed, and their origins extensive in the Australian aboriginal. They each had a superficial and a deep insertion into the modiolus, and were closely approximated to the M. orbicularis oris.

In the Sunda Islander, Koster found both the M. incisivus superior and inferior to be present and well developed.

Other observers do not specially mention these muscles.

*M. mentalis.* This muscle was powerfully developed in the Australian

aboriginal but agreed with Virchow's description in the European, inasmuch as it enclosed a fibrous pad, though no pad of fat was seen. The M. anomalus menti and M. praemandibularis transversus formed a large though pale and thin-fibred fan-shaped sheet.

Koster found a M. praemandibularis rectus (M. anomalus menti (?)) in the head of one Sunda Islander.

L. Harslem-Riemschneider found no peculiarities in the Papuan, except that the muscle was often powerfully developed.

Zeidler found the muscle powerfully developed in the Herero and Hottentot, but not widely different from the European.

Fetzer found no peculiarities.

*M. orbicularis oculi.* This includes the pars peripheralis (or M. malaris) which corresponds in large part to the fasciculi deflexi (A 1 and A 2 and B 3) of Loth and others.

In the Australian aboriginal, the whole M. orbicularis oculi was very much larger in extent than in the European, covering not only the M. zygomaticus laterally, but medially the various capita of the M. levator labii superioris, and in addition forming a well-marked M. oculo-buccalis.

Below and lateral to the orbit, the lateral fibres became inextricably bound with the fibres of the M. zygomaticus. The oval or circular fibres appeared to extend lower and more laterally in the molar region than in the European. A comparison of our measurements of the muscle with those collected by Kudo is difficult, as the greatest vertical width of the muscle does not lie at the centre of the palpebral fissure, but considerably lateral to this.

It can be stated, quite definitely, however, that there is a marked increase laterally, the measurements of the muscle width in this region exceeding those recorded for the Negro, Japanese, Chinese and European.

A comparison of Koster's measurements in two Sunda Islander heads (Javanese) is of interest. Whereas the greatest dimension of the muscle is lateral in the aboriginal, in the Sunda Islander it is inferior or caudal.

The fasciculi deflexi A 2, as described by Koster, corresponds exactly to the caput laterale M. malaris. The Sunda Islander resembles the Australian aboriginal in that both capita were well developed, including the M. oculo-buccalis.

L. Harslem-Riemschneider found the muscle powerfully developed in the majority of cases in the Papuan and Melanesian. The M. malaris also appeared to be well developed.

As far as can be determined from Zeidler's description the M. malaris (fasciculi deflexi) was not well developed in the Herero, except perhaps in the child.

Fetzer found the M. malaris almost invariably well developed in the Hottentot, more especially the caput mediale.

*M. depressor capitis supercilii.* This muscle was very well developed with a wide lateral extension in the Australian aboriginal.

Kudo found no difference between the Chinese and the European and from an examination of his figures it seemed to be weakly developed as compared with the Australian aboriginal.

In the Sunda Islander it appears from Koster's figures to be well developed and similar to that of the Australian aboriginal.

Neither Harslem-Reimschneider, Zeidler, nor Fetzer describe this muscle.

*M. corrugator supercilii.* This muscle was well developed in the aboriginal, with a very extensive bony origin. In the Mongolian, according to Kudo, the muscle was not specially developed and was difficult to separate from surrounding muscles.

In the Sunda Islander, the muscle was very well developed.

Zeidler found the muscle well developed in the Herero in all cases.

Fetzer found no difference between the Hottentot and the European.

*M. procerus.* This muscle was well developed in both aboriginal heads, and bilaterally symmetrical in one head.

Kudo found it invariably well developed in the Mongolian.

Koster found it well developed in the Sunda Islander, and its narrowest breadth in two heads was the same as that found in H. B. 1 (e.g. 0·9 cm.).

L. Harslem-Riemschneider found the muscle well developed in the Papuan and Melanesian.

Zeidler found the muscle well developed in the Herero.

Fetzer found no special peculiarity in the M. procerus in the Hottentot.

*M. frontalis.* No special peculiarity was observed in the aboriginal, except that there was no separation of the muscle into two halves in the middle line, nor were the medial fibres appreciably shorter than were the lateral.

Kudo found no special peculiarity in the Mongol, though a separation into two halves was never observed, nor did Koster observe anything special in the Sunda Islander.

L. Harslem-Riemschneider found considerable variation in the relationship of this muscle to the upper border of the M. orbicularis oculi, in the Papuan and Melanesian. A portion of the muscle, especially medially, sometimes passed superficial to the fibres of the M. orbicularis oculi.

Zeidler found in the Herero and Hottentot that the muscle was well developed, and its length was as much as 108 mm., being considerably greater than that found by ourselves or other observers.

Fetzer found no special peculiarity in 17 Hottentot heads.

*M. occipitalis.* This muscle was not powerfully developed in the Australian aboriginal; in one head (D. B. 2) the posterior auricular musculature was complete, but did not correspond to the auricular-occipitalis group of muscles usually described in this region.

Comparison with Kudo's measurements of Mongols and Europeans confirms the above statement about the development of this muscle. Contrary to the usual findings, the M. occipitalis partly covered the uppermost belly of the M. auricularis posterior.

Zeidler and other observers found the muscle much more powerfully developed in the Herero and Hottentot, and suggest that this may be associated with dolichocephaly. Such a suggestion is not, however, borne out by our limited observations on the Australian aboriginal.

Fetzer found great variation in 17 Hottentot heads.

The extreme variability of all the auricular muscles, especially those lying posteriorly, make any comparisons difficult.

*Auricular muscles.* The extreme variability of all the auricular muscles, especially those lying posteriorly, make any comparisons difficult.

# THE AGE ORDER OF THE APPEARANCE AND UNION OF THE NORMAL EPIPHYSES AS SEEN BY X-RAYS

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ABBREVIATIONS

E. = epiphyses
A.P. = antero-posterior
tr. = transverse
y. = year
m. = month

## I. INTRODUCTION

It is well known that the age order of appearance and union of epiphyses as set forth in the standard textbooks of anatomy is not strictly correct in all details. We do not doubt that the majority of statements are true, but while collecting X-ray plates for a Radiological Museum of normal epiphyses for the Anatomy Department, we found in certain cases such a widely-divergent appearance from that usually set forth in the textbooks that we determined to enquire more into the matter and to see if any satisfactory result could be obtained. With the permission of Dr Fildes of the X-ray Department, we examined a series of X-ray plates taken from that Department. These plates were those taken of all patients in the ordinary course of treatment at the Hospital. Any plate which showed a pathological change was discarded. We were able to obtain the *age* in *years* of all persons from whom the plates were taken. We could not get nearer in age than this in the majority of cases, except those which we had specially X-rayed for the Radiological Museum. This method was unsatisfactory in the fact that we could not obtain any data as to the patients' physique, e.g. the height, sexual characteristics, etc. We have ignored the epiphyses in the skull, scapula and vertebral column which do not lend themselves to this form of enquiry, and most of our data are concerned with the long bones.

This investigation, therefore, is not a complete one, and we recognise the need for more evidence on the union of the long bones and the appearance of the epiphyses in the long bones of the hand and foot.

It will be seen that we often give the size in millimetres of the epiphysial centres, a proceeding which is open to the criticism that the size of the structure on the X-ray film is not necessarily that of life owing to the divergence of the rays and the varying distance of the ossification above the film. We admit the justice of this criticism but have satisfied ourselves, however, that the error is so slight that much is gained by the practice; since the approximate size of the structure often gives a clue to the length of time during which it has been present. In any case it is clear that the actual size never can be more than that stated: though sometimes it may be a little less. Altogether more than 5000 X-ray plates were examined.

In the account which follows we describe the age and the appearance of the epiphyses of each bone separately. We give a table of our results, which are summarised at the end.

## II. DESCRIPTIVE ACCOUNT OF INDIVIDUAL EPIPHYSES

### *The Humerus*

*The Upper End.* The head of the humerus was present in 2 out of 4 cases which we have seen at birth. In each, it was 2 mm. in width. In a child aged 2 days, it was 2 mm. in width and thus must have been present at birth. At the 8th month it is 9 mm. in width and from thence onwards it was found to be always present. We have no observation between the 2nd day and 8th month. By 2 y. 8 m. it has reached a width of 18 mm.

The great tuberosity was first seen at 8 m. (4·5 mm. in width) and was seen also at 9 m. and 12 m. Then it was absent at 12, 15 and 16 m., present at 16 m. (10 mm. wide), absent at 18 and 18 m. and then present at 21 m., and from thence onwards in our observations. This differs considerably from estimates given in textbooks, which put the appearance of the great tuberosity in the 3rd year (see Table at end). The union of the great tuberosity with the head shows a fairly wide variation. Our first observation of union is at 4 y. 11 m., separate at 5, 6, 6 y., and is completed at 6 y., and from thence onwards, except for one case at 12 y. when the head and great tuberosity are distinctly separate. Taking an average, the commonest time of union is in the 7th year, though it may occur at any age between 5 and 7.

We have never seen a centre for the lesser tuberosity. Its separate existence must be transitory and we think that a series of radiograms between the ages of 4 and 6 may possibly reveal its presence, though we have grave doubts as to whether it is of constant occurrence. The junction of the head and great tuberosity occurs between 19 and 21 y. The earliest union we have seen is at 18 y. 2 m. with no epiphysial line present, and the latest at 21 y., though we need far more observations between these ages.

*The Lower End.* Our first observation of the capitellum was at 12 m. (♀) and at 15 m. (♂). It was absent at 15 and 18 m., and then present at 18 m.

(♀—4 mm. A.P.), and always present from thence onwards. In one case of a girl of 2 y. there was a second epiphysis present, which we had every reason to believe was not the internal epicondyle.

The internal epicondyle was first seen at 3 y. 9 m. (5 mm. vert. 3 mm. tr.), then at 4 y. 11 m., absent at 5 y., present at 5 y., and from thence onwards. In a specimen of a girl of 13 y., the epiphysis was situated largely behind the epicondyle, a position which we believe it always occupies.

The trochlear centre was first seen at the 10th year, and we have 5 observations of its presence at that time, while in 2 observations at the 11th year it was absent. Textbooks usually put its appearance at the 12th year.

The external epicondyle was first seen in the 11th year (present in 3 out of 7 observations in that year). From thence onwards it is always present. Textbooks place its appearance at the 14th year.

The fusion of the capitellum trochlea and the external condyle is first seen in the 13th to 14th year, while their junction to the shaft was first noticed at 16 y. 4 m., and from thence onwards in our observations. The internal epicondyle remains separate up to the 20th year, except for one observation at 18 y. 2 m. when it was distinctly joined. It is an open matter whether this epicondyle joins the shaft before or after the head of the humerus.

### *The Radius*

*The Upper End.* The first observation of its appearance is at 2 y. (♀), absent at 3 y. 6 m. (♂), present at 3 y. 9 m. (♀), and from thence onwards always present. In one specimen at 7 years it was just appearing (a minute speck) though the average size at that age is 10 mm. A.P. We should put the average age of its appearance in the 4th year.

The earliest observation of junction was at the 14th year and afterwards at the 15th, 16th, 17th, 18th years. In 3 observations at 15 y. 10 m., 16 and 19 y., it was still separate. We should put the average age of junction as the 15th to 16th years. We have no evidence of the appearance of a separate E. for the tuberosity of the radius.

*The Lower End.* It was first observed at 10 m. (♀) 3·5 mm. tr., then at 12 m. ♂ (4 mm. tr.) and then out of 15 observations in the 2nd year it was absent only twice (at 15 m. and 17 m. both ♂). Since of 4 observations at 12 m. and 3 observations at 13 m. the average size was 5·7 mm. tr., we can safely say that the time of appearance of this epiphysis is *at the end of the first year* (10 to 12 months) and the beginning of the second.

From the 8th to the 10th years the epiphysis becomes flush with the margins of the shaft and occupies the whole cartilaginous epiphysial mass except the epiphysial line. This condition we propose to speak of as complete. About this age, too, the styloid process begins to appear. Union may begin as early as the 17th year but the commonest time is the 19th–20th year. In 4 specimens of 20 y., union had taken place in all; though in another specimen at 22 y. union was not complete.

### *The Ulna*

*The Upper End.* Our first observation of its appearance is in the 11th year, as in 8 cases it was present 5 times, and its size varied from 3 to 11 mm. A.P. In 3 observations of the 10th year it was *not* present.

Thus, the average time of the appearance of this centre may be ascribed to the 11th year. Occasionally it is delayed and in 1 case was absent in the 13th year. In 3 cases, 2 epiphyses were present, one above the other, the smaller one being above. It is definitely separate up to the 15th year; in 2 cases in the 16th year it is joined anteriorly and not posteriorly, and this was also seen again in the 19th year. In the 20th year it was completely joined and no E. line was visible. We have not made sufficient observations of this union to be dogmatic, but would suggest that the complete union occurs a little later than that suggested by the textbooks, 15th–16th year, and would place it in the 17th year.

*The Lower End.* The date of appearance of this epiphysis is usually given as the 4th year. We think this is wrong, and much too early. Twenty-seven observations up to the 6th year showed its presence only once (at 5 y. 6 m.—4 mm. tr. ♂). In 7 observations in the 7th year it was present only 3 times, and in 5 observations in the 8th year it was present only twice. In 1 observation in the 9th year it was absent. We may say that its average appearance is between the 7th and 8th years.

The styloid process begins to ossify on an average about the 10th to the 11th year and is not complete until the 16th year. In 2 cases out of 45 the epiphyses were double, the two centres being side by side.

### *The Carpus*

*The Os Magnum.* The centre for this bone was first seen at 3½ m. (3 mm. tr.) and was the only ossification present in the carpus. At 4 m. (4 mm. tr.) it was again seen together with the unciform (2 mm. tr.). At 5 m. it was present with the unciform, and at 6 m. it was alone. In another observation at 6 m. it was present with the unciform and from thence onwards the unciform was always present with it, except for one observation at 15 m. when it was the only carpal bone present. The average time of appearance we would put at the 3rd to 5th month, about a month ahead of the unciform. The centre is oval with a vertical long axis, and during the 1st year this axis has not been of a greater length than 7 mm.

*The Unciform.* The first appearance of its centre was at 4 m., absent at 5 m., present at 5 m., absent at 6 m., present at 6 m., and from thence onward always present. We have never seen the unciform present without the os magnum. It is generally 1 to 2 mm. smaller than the os magnum but may be larger (2 cases out of 18). We put the average appearance between the 4th and 6th month.

*The Cuneiform.* The appearance of its ossific centre is subject to a good deal of variation. It was first seen at 12 m. (♀), and then seen in 7 out of 14 observations in the 2nd year, 5 times out of 12 observations in the 3rd year, and 5 times out of 8 observations in the 4th year. From the 5th year onwards it was constantly present.

From the data we have we cannot put the appearance more definitely than between the 2nd and 4th years.

*The Semilunar.* This bone was first seen at 23 m. (the only appearance in the 2nd year). Out of 12 observations in the 3rd year it was seen twice, in 8 observations in the 4th year it was seen 4 times, and in the 5th year and afterwards it was always present except for one observation in the 5th year. We would put the average appearance between the 3rd and 4th years, but more definitely in the 4th year.

*The Scaphoid.* This bone was not seen until the 5th year. In 4 observations of that year it was present twice. In 6 observations in the 6th year it was present only twice. In 6 observations in the 7th year it was present 5 times, and in 3 observations in the 8th year it was not present at all. Thereafter it was always present except for one observation in the 9th year. It is difficult to correlate its appearance 5 times out of 6 in the 7th year and entirely absent 3 times out of 3 in the 8th year. We need more observations in the 8th year before we can be more definite on this subject, but with the material at hand we put the average appearance of the scaphoid as in the 7th or 8th year.

*The Trapezium.* In 8 observations in the 4th year it was seen once (3 y. 9 m.—3·5 mm. tr. ♀). In 4 observations in the 5th year seen twice; in 6 observations in the 6th year, seen 3 times; in 6 observations in the 7th year, seen 4 times, while in the 8th year it was constantly present and from thence onwards.

*The Trapezoid.* This bone was first seen in the 5th year and was present in 1 out of 4 observations (4 y. 11 m. ? sex). In the 6th year it was present only once out of 6 observations. In the 7th year it was present 4 times out of 6 observations. In the 8th year either itself or the trapezium was present in 2 out of 3 observations. In the 9th year and afterwards it was constantly present. It is often very difficult in X-ray observations to be sure whether one is dealing with the trapezium or trapezoid since the hand is often in a position in which the former is directly in front of the latter. For this reason many of our data in the appearance of these bones must be accepted with caution. When both bones are reported present or both absent this observation is trustworthy, but when only one is recorded it may quite well be the other.

Still, we believe that the ossification in the trapezium begins before that in the trapezoid and would put the average ossification of the trapezium as in the 6th to 7th year, while that of the trapezoid as in the 7th to 8th year.

*The Pisiform.* The presence, or still more, the absence of this bone is often difficult to determine in an X-ray plate. It was first observed in the 12th year

and was constantly present afterwards. It appears to be much more constant in its appearance than most of the carpal bones. We have no reason to doubt that the 12th year is the usual time of appearance.

### *The Metacarpals*

*The 1st Metacarpal.* The epiphysis for this bone was not seen during the 1st year. In 11 observations in the 2nd year it was present twice, together with the epiphysis of the 2nd, 3rd and 4th metacarpals. In 12 observations in the 3rd year it was present 8 times together with all the epiphyses of the other metacarpal bones, while in the 4 times it was absent all the other epiphyses of the metacarpal bones were also absent. After the 3rd year it was always there. So we safely put the average appearance of this bone as in the 3rd year.

The epiphysis becomes complete in the 9th year. The first evidence we have of junction is in the 16th year (once out of 5 observations). Out of 8 observations in the 17th year it has joined in only 2. In all observations in the 18th year it has joined and remains so from thence onwards except for one case of 22 y. when it was still complete and separate. We would put the average age of union as the 18th year.

*The 2nd, 3rd, 4th and 5th Metacarpals.* The first observation we have is in a girl of 12 m. in which the heads of the 3rd and 4th metacarpals are present. Later at 13 m. (♂) the 2nd, 3rd and 4th are present, but not the 1st and 5th. At 15 m. (♀) the 1st, 2nd, 3rd and 4th are present, but not the 5th. At 18 m. the index alone is present. At 23 m. the 2nd, 3rd, 4th and 5th are present but not the 1st. Out of 11 observations in the 2nd year, the heads of the metacarpals are present 3 times. Out of 13 observations in the 3rd year, the heads are present 8 times. In the 4th year they are present in all cases—5 out of 5—and are present from thence onwards.

We may safely state that the average appearance is in the 3rd year, though some cases appear in the 2nd year.

In order, the index appears first, as in 1 case it alone was present, while in 3 others it was larger than any of the others. Judging by measurement it appears almost certain that they come in their numerical order, beginning with the 2nd and ending with the 5th. It is not until the 9th year that the epiphyses are complete. Union seems to occur in the 18th year (5 observations), and we are indebted to Commander Pickering Pick for a series of observations on Dartmouth cadets in the 17th year in all of whom no union had taken place.

### *The Phalanges*

*The Proximal Row.* The epiphyses for the first row are said to appear in the 3rd to 4th year according to Gray, but they often appear much earlier than this. We saw them in a child of only 9 m., when all were present. At 12 m. the index and medius alone were present, the index being the longer. At 15 m. the index, medius and annularis were present, the index being the

longest. At 18 m. this was seen again, and in neither case were any epiphyses for the middle and distal rows seen. The study of our records leaves little room to doubt that the order of appearance is index, medius, annularis and then minimus or pollex, though our evidence does not allow us to be sure of which. In 2 cases the proximal epiphysis of the thumb shows two centres side by side.

In 8 observations in the 2nd year they were present in 4. In the 4 observations in which they were absent, it was the first half of the year. In the 3rd year they were present in 6 out of 7 observations.

We would put the average appearance of the proximal row as the end of the 2nd year and beginning of the 3rd year (18th month to 30th month).

*The Middle Row.* These were first observed at the end of the 2nd year and were present in 2 out of 8 observations in this year (22 m. and 23 m.). In the 3rd year they were present in 4 out of 5 observations. Again the order of appearance is the same as the proximal row.

We would put the average appearance as the beginning of the 3rd year, and just a little after the proximal row.

*The Distal Row.* These were present once out of 8 observations in the 2nd year (23 m.). They appear a month or so later than the middle row as at 22 m. only the proximal and middle were present, while at 23 m. they were all present. In the 3rd year they were present in 4 out of 5 observations.

We would put the average of appearance as the beginning of the 3rd year, just after the middle row.

We have seen no X-ray in which the distal epiphyses are present without the middle and proximal, or the distal and middle epiphyses without the proximal.

Taking all the phalanges, their epiphyses appear in their numerical order, the proximal first (18 m. to 2 y. 6 m.), the middle next (22 m. to 2 y. 6 m.) and then distal (2 y. to 3 y.). In each row they also appear in the order of index, medius, annularis and minimus or pollex.

The first observation at union was at 16 y. 9 m., and then at 17 y. when the distal row had joined but not the middle or proximal.

Of 4 observations in the 18th year they were all joined, and we have not seen any separate beyond that age. We would put the age of union as the 18th year in the order of distal, middle and proximal.

### *The Femur*

*The Upper End.* The head was first observed at 6 m. (♀) and was then 1 mm. wide, and another case at 9 m. (? sex) and was 9 mm. wide. From the 6th month onwards it was always present.

The great tuberosity was first seen in the 4th year (5 mm. tr. ♀) and from thence onwards was always present, except for 1 case of 5 y. in which it was definitely absent.

At 5 y. the head of the femur is so large that the epiphyseal line is marked out and is always *horizontal.* At 6 y. the head and the great tuberosity have

reached the limits of the pre-existing cartilage, and so are complete. By the 7th year the apophysial part of the lesser trochanter is present but no epiphysis.

The lesser trochanter was first seen in the 10th year (once out of 4 observations of that year). It was absent in 4 observations in the 11th year. It was next seen in the 12th year (3 out of 4 observations). In the 13th year it was present in 3 out of 4 observations (the 4th was queried). In the 14th year out of 3 observations it was definitely present once while the other 2 were indefinite. We would put the average appearance of the lesser trochanter from the 12th–14th year, and would say that it appears earlier than the usual statement in the textbook—i.e. the 14th year.

By the 11th year the epiphysial line of the head of the femur is *oblique* and not *transverse*.

*Union.* The lesser trochanter was just seen to be joined in the 16th year and then in the 17th and from thence onwards. We would put the union at the 17th year.

The great trochanter was first seen joining above and separate below at 15 y. 10 m. and was joined at 16 y. 4 m. and 18 y. 4 m.

The first observation of union of the head was at 16 y. 4 m. when it was completely joined and no epiphysial line was present. Then again at 18 y. 2 m. it was joined. We have not enough material to make any definite statement as to the most usual time of union of the head and great trochanter, but from what evidence we have we would suggest 18–19 y. for the great trochanter and 19–20 y. for the head.

*The Lower End.* In the X-rays at birth the epiphysis is always present with an average size of 8·5 mm. tr. We have *no* observation of pre-natal stages, so cannot say when this epiphysis first appears.

At 6½ y. the epiphysis is complete, the epiphysial line has a wavy course, convex upwards in the middle and concave at each side.

The first indications of union we have are in the 17th year when in 2 observations union was occurring though the epiphysial line was definitely present. Of 4 observations in the 18th year the epiphysis was still separate. Of 4 observations in the 19th year, 3 had completely joined and no epiphysial line was visible, while the other was still uniting. After this age observations showed that the epiphysis was united. We would put the age of union at the 19th year.

### *The Tibia*

*The Upper End.* In our observations at birth the centre for the upper extremity is *always* present and ossified, with an average size of 7 mm. tr. We have no ante-natal observations and so cannot state at which period the centre for the head first appears. We should like to emphasise its constant appearance at full-term birth, and from a medico-legal point of view its presence is of as great importance as the lower end of the femur. In the 9th year the epiphysis is complete. The first evidence of its union that we

have is at 15 y. and then at 16 y. 8 m., but in 5 observations in the 18th year it is still unjoined. In the 19th year it is uniting and in the 20th joined definitely. We would put the age of union as at the 19th–20th year.

*The Anterior Tubercle.* This was first seen in the 11th year, and was noticed as a small projection growing down from the epiphysis of the head. The tubercle was constantly present after this except for 2 observations—one in the 13th year and another in the 14th year, when it was unossified in both cases.

In several cases the tubercle appeared as a separate epiphysis—not attached to the head or the shaft (at 10, 11, 12, 13, 15). In another case of 13 y. ♀, the tubercle was joined to the head above and the shaft below, but separate in between. In yet another case an extra epiphysis was seen, being in front of the tongue-like process of the tubercle and being in the substance of the lig. patellae.

The tubercle remains separate from the shaft up to the 17th year and the first evidence of its union was seen at 16 y. 8 m. At 17 y. it was again separate, and in another observation at this year it had united. In another observation at 17 y. it was completely unossified. In all observations after the 18th year it was completely joined. We would put the age of union at the 18th year, though we would like more evidence to confirm this.

*The Lower End.* This was first seen at the end of the 1st year, and out of 5 observations in the 1st year from the 9th month onwards it was present in all. From this time onwards it is always present. Since at 9 m. it was 12 mm. tr. in size it must have been present for several months before, and so we are safe in putting the appearance of the lower end of the tibia at the latter half of the 1st year (6th to 12th month). The epiphysis is complete by the 6th year.

In the beginning of the 7th year the internal malleolus starts to ossify and at the 12th year is complete.

The first evidence of union is in the 16th year and of 7 observations in the 17th year, 6 have united and the evidence we have of the 18th and 19th years shows complete union.

We would put the age of union as between the 17th and 18th years.

### *The Fibula*

*The Upper End.* The earliest appearance of this epiphysis we have seen is in the 4th year, and then it was only present once out of 3 observations. In 4 observations in the 5th year it was present only once and that at 4 y. 11 m. It was present in all observations in the 6th year, and from thence onwards. We would put the date of appearance as in the 5th to the 6th year, more commonly in the 6th. At the 11th year the epiphysis is complete.

The union of this epiphysis with the shaft is later than that of the head of the tibia. All our observations up to and including the 20th year show that it is still separate, and all we can say is that it joins after that time.

*The Lower End.* This epiphysis was first seen at the 11th and 12th month, was absent in an observation at 13 m., and after that time always present. We would put its appearance at the end of the 1st year and beginning of the 2nd year.

In the 7th year the epiphysis is complete.

The first evidence of union is in the 17th year (2 observations) and then all observations in the 18th and 19th years show union. We would put the age of union as the 18th to 19th year.

### *The Tarsus*

*The Astragalus.* It was present at birth in all observations. We have no ante-natal records to state its exact time of appearance.

*The Os Calcis.* The primary centre was present at birth in all our observations, and we have no ante-natal records to state its exact time of appearance.

*The Post Epiphysis.* It was first seen in the 10th year as a few specks in the epiphysial cartilage. In another observation in the 10th year it was 6 mm. vertical in size. From the 10th year onwards it is always present. The appearance of the epiphysis is variable. In 2 cases it appears to ossify from below upwards and the epiphysis occupies to start with the lower half of the posterior surface of the os calcis. These 2 cases were in the 10th year. In 3 cases in the 12th year and 4 cases in the 14th and 15th years there were two separate centres, one above the other. We believe that it generally ossifies in two centres, the lower one appearing first in the 10th–11th year and the upper in the 12th–14th years. The two centres coalesce in the 15th and 16th years, and the epiphysis is complete at the end of the 16th year, i.e. it occupies the whole of the posterior surface of the os calcis.

The first evidence we had of union was at 15 y. 9 m., when an observation at that age showed complete union. Out of 6 observations in the 17th year, 4 were united and 2 not united. We may put the age of junction at the 17th year in the majority of cases.

*The Cuboid.* We have *not* seen the cuboid present at birth in any of our observations. It was first seen at 4 m. and was always present from thence onwards. We would put its appearance as in the first 4 months of life.

*The External Cuneiform.* This also was first seen at 4 m. and was present always from thence onwards. Whether it appeared before or after the cuboid we cannot say until we have more observations between birth and 4 m. Since the cuboid was large in size in the case quoted, we may assume that it appeared before the cuneiform. We would put its appearance in the first 6 months, a little after the cuboid.

*The Internal Cuneiform.* This was first seen at 12 m. (2 mm. tr. ♀), was absent at 15 m. (♂), present at 18 m. (2 mm. tr. ? sex), absent at 2¼ y., present at 2 y., and from thence onwards present. We would put its appearance as the *end of the 2nd year.*

*The Navicular.* It was first seen at 18 m. (6 mm. tr.), then at 2 y. (3 mm. tr.),

absent at 2¼ y., but present from thence onwards, except in 2 cases at 3 y. We would put its appearance as the beginning of the 3rd year.

*The Middle Cuneiform.* It was first seen at 2 y. (2 mm. tr. ♀), and was present from thence onwards except in 1 case of 3 y., where it was absent together with the navicular. We would put its time of appearance as the 3rd year.

It is difficult to say which appears first, the navicular or the middle cuneiform. We believe that the navicular comes just before the middle cuneiform, as the following table of sizes will show:

| Age | Navicular | M. cuneiform |
|---|---|---|
| 18 m. | 6 mm. tr. | Absent |
| 2 y. | 3 mm. tr. | 2 mm. tr. |
| 2 y. 6 m. | 7 mm. tr. | 4 mm. tr. |
| 2 y. 8 m. | 4 mm. tr. | 7 mm. tr. |

Out of these 4 observations the navicular is larger in 3 cases, and suggests that it appears just before the middle cuneiform. That statement is contrary to that in most textbooks in which the navicular is last to appear. We would put the order of the tarsal bones as follows:

| | |
|---|---|
| Os calcis ... ... ... | Present at birth |
| Astragalus ... ... | Present at birth |
| Cuboid ... ... ... | 1st to 4th month |
| External cuneiform ... | 1st to 6th month |
| Internal cuneiform ... | End of 2nd year |
| Navicular ... ... ... | 3rd year (beginning) |
| Middle cuneiform ... | 3rd year |

### *The Metatarsus*

We have very little evidence on the appearance of the epiphysis of the metatarsal bones on which to base any definite statements. The first observation is at 10 m. ♀, when the base of the 1st and head of the 2nd are present, but no others. In 3 observations in the 2nd year they are *all* absent. Of 3 observations in the 3rd year, the base of the 1st was present twice (2 y. ♀—3 mm. tr. and 2 y. 8 m. ? sex—3·5 mm. tr.), but no other epiphysis was seen.

In the 4th year, of 2 observations, no epiphysis was seen in one, while in the other the base of the 1st metatarsal alone was seen.

The next observation was at 4 y. 11 m. when they were all present, and after that time they were always present.

In the 7th year the epiphysis was complete.

The first evidence of union was in the 17th year (16 y. 4 m. ♂), when they were all joined, but in another observation at 16 y. 6 m. they were all separate. At 18 y. 2 m. they were all joined. The evidence we have of union and appearance is scanty, but we would suggest tentatively that the epiphyses appear in the 4th and 5th years with the bone of the 1st metatarsus appearing first, while we have no evidence as to the appearance of the remaining epiphyses

of the heads of the metatarsals. We would suggest that union occurs in the 17th–18th year.

### *The Phalanges*

Here again our evidence is very scanty. The first evidence we have is at 2 y. ♀, when the proximal row alone are present. At 2 y. 6 m. ♂, there are no epiphyses present. The next observation we have is at 6 y. 1 m. ♀, when all rows are present. On this very slender evidence we can only suggest that the proximal row appears first and in the 3rd to 4th year, while the middle and distal appear later and are certainly present before the 7th year. Evidence of union is again scanty. At 15 y. ♂, the phalanx of Hallux is joined, while the remainder are separate. At 15 y. 6 m. the minimus is joined in the middle and distal rows while all the others are separate. At 15 y. 10 m. the 1st and 2nd of the proximal row are joined, 4th and 5th in the middle row, and all the distal, while the remainder are separate. At 16 y. 4 m. they are all united. At 18 y. 2 m. all united.

On this we can base little, except that union may start in the 16th year and be complete in the 19th year. It is not enough evidence on which to give the order of union.

### *The Os Innominatum*

We have directed our attention here to 3 observations:

(1) The Sub-Pubic Junction;
(2) The Ilio-Isch. Junction;
and (3) The Crest of the Ilium.

Of these most of our attention has been directed towards the sub-pubic junction.

*The Sub-Pubic Junction.* At 15 m. this junction is separate, and the bones are 10 mm. apart. At 2 y. it is separate. At 3 y. ♂ it is definitely joined. Of 5 observations in the 4th year, 3 are separate, and 2 joined. In one of the joined is a distinct heaping up of bone at the junction. Of 8 observations in the 5th year, 3 are joined on both sides, 2 are joined on one side and not on the other, while 2 are separate and the last just joining. In 2 of the specimens which were joined there was distinct heaping up of bone. Of 7 observations in the 6th year, 3 were joined, 2 were joining, and 2 separate. Of 4 observations in the 7th year, 2 were separate (2 mm. gap) and 2 joined.

In the 8th year and afterwards all specimens were joined, and up to the 10th year heaping up of bone occurred at the junction. After the 10th year there was no heaping of bone and the union was even.

All we can say about the junction is that after the 7th–8th year union occurs, but it may occur much earlier than this, even up to the 4th year.

*The Ilio-Isch. Junction.* The first observation of junction we had was at 16 y. 4 m. After that at 18 y. 2 m. it was joined. All we can say is that union occurs after the 17th year.

*The Crest of the Ilium.* This was first observed in the 18th year (absent in the 16th and 17th) and remained separate until the 23rd year. We have no evidence of its exact time of union, nor whether it ossifies from two centres.

## III. CONCLUSIONS

Many of our observations are incomplete, especially with reference to union in certain of the long bones, and the times of appearance of the epiphyses in the long bones of the foot. We should like to lay much stress in this communication on the age order of the appearance of the epiphyses, rather than on the union, as our observations are far more complete at the earlier ages, and also because it is not always possible to be sure in an X-ray film whether complete bony union has taken place.

Certain facts stand out:

1. That the epiphyses of the long bones appear earlier than usually stated in the textbooks, with one exception of the lower end of the ulna. This usually is stated to appear in the 4th year, while we have not seen it until the 7th–8th, rather in the 8th year. The only supporting evidence we have is that of Dorland (from Pryor) who puts it in the 6th–8th year.

The epiphyses which appear earlier are as follows:

(*a*) Head of humerus at birth and not 1st year.
(*b*) Lower end of radius at 1st year and not 2nd year.
(*c*) External condyle of humerus at 11th–12th year, and not 14th year.
(*d*) Capitellum, 2nd year and not 3rd year.
(*e*) Great tuberosity, 1st to 2nd year and not 3rd year.
(*f*) Phalanges of hand, 2nd–3rd year and not 3rd to 5th year.
(*g*) Lesser trochanter of femur, 12th–14th year and not 14th year.
(*h*) Upper end of tibia, before birth and not *at* birth or 1st year.
(*i*) Lower end of tibia and fibula in 1st year chiefly and 2nd, and not 2nd year.
(*j*) Cuboid appears after birth and not before (Pryor).
(*k*) Internal cuneiform in 2nd year and not 3rd year.
(*l*) Navicular and middle cuneiform in 3rd year and not 4th year.
(*m*) The sub-pubic arch joining at 8th year or much earlier, and certainly not at 15th year as suggested by Stevenson.

2. The varied appearance of the epiphyses of the os calcis fragmentation and double epiphysis.

3. That the female epiphyses appear before the male. This has been borne out by many observations. For instance, when an epiphysis appears very early and then there is a long gap before it appears again, this early appearance is almost invariably female; or, with two X-rays of the same age but different sex, the female will show the epiphyses while in the male it is absent; or, again, with two plates of the same age, the female epiphysis is invariably a little larger than the male.

4. The appearance of double epiphyses for:
   (1) The proximal phalanx of the thumb (2 observations).
   (2) The lower end of the ulna (1 observation).
   (3) The upper end of the ulna (3 observations).
5. The varied appearance of the anterior tubercle of the tibia.
6. No double or extra epiphyses has been seen in any of the carpal bones.

## IV. SUMMARY

| Bone | Appears | Joins |
|---|---|---|
| **Humerus** | | |
| Head | Birth | 19–21 |
| Great tu. | 1–2 | 19–21 |
| Lesser tu. | ? | 19–21 |
| 1. Cap. | 2 | 17 |
| 2. Int. con. | 5 | 20 |
| 3. Troch. | 11 | 17 |
| 4. Ex. con. | 11–12 | — |
| (1, 3 and 4 fuse at 14) | | |
| **Radius** | | |
| Upper | 4 | 15–16 |
| Lower | 1 (10–12 m.) | 19–20 |
| **Ulna** | | |
| Upper | 11 | 17 |
| Lower | 7–8 | 20 |
| **Carpus** | | |
| Os. magnum | 3–5 m. | — |
| Unciform | 4–6 m. | — |
| Cuneiform | 2–4 | — |
| Semilunar | 3–4 | — |
| Trapezium | 6–7 | — |
| Scaphoid | 6–8 | — |
| Trapezoid | 7–8 | — |
| Pisiform | 12 | — |
| **Femur** | | |
| Head | 6–12 m. | 19–20 |
| Great troch. | 4 | 18–19 |
| Lesser troch. | 12–14 | 18 |
| Lower end | Before birth | 19 |
| **Tibia** | | |
| Upper | Before birth | 19–20 |
| Lower ant. | 6–12 m. | 17–18 |
| Tub. | 11 | 17–18 |
| **Fibula** | | |
| Upper | 5–6 | 20–22 |
| Lower | 1–2 | 18–19 |

| Bone | Appears | Joins |
|---|---|---|
| **Tarsus** | | |
| Os. cal. | Before birth | — |
| E. of os. cal. | 10 | 17 |
| Astrag. | Before birth | — |
| Cuboid | 1–4 m. | — |
| Ex. cun. | 1–6 m. | — |
| Int. cun. | 2nd y. (end) | — |
| Navicular | 3rd y. (beg.) | — |
| Middle cun. | 3rd y. (mid.) | — |

| Bone | Appears | Order | Joins |
|---|---|---|---|
| **Metacarp.** | | | |
| 1st | 3 | 1 | 18 |
| 2nd | 3 | 1 | 18 |
| 3rd | 3 | 2 | 18 |
| 4th | 3 | 3 | 18 |
| 5th | 3 | 4 | 18 |

| Bone | Appears | Joins |
|---|---|---|
| **Phalanges** | | |
| Proximal | 18 m.–2½ y. | 18 |
| Middle | 22 m.–2½ y. | 18 |
| Distal | 2–3 | 18 |
| **Metatarsus** | | |
| 1st | 3–4 | 18 |
| 2nd | 4–5 | 18 |
| 3rd | 4–5 | 18 |
| 4th | 4–5 | 18 |
| 5th | 4–5 | 18 |
| **Phalanges** | | |
| Proximal | 3–4 | 17–19 |
| Middle | 3–4 | 17–19 |
| Distal | 4–6 | 17–19 |
| **Os innominatum** | | |
| Sub-Pubic | — | 7–8 |
| Ilio-Isch. | — | 17– |
| Crest of Ilium | 18? | 23– |

The numbers are in years except when stated otherwise.

# THE DEVELOPMENT OF MUSCLE IN THE HUMAN FOETUS

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THE histogenesis of muscle in the human has not, as far as the author is aware, been hitherto described in detail, although the process has been followed in considerable detail in certain other mammals. Thus McGill (1) gives a full account of the development of smooth muscle in the pig, the process being similar to that described below. The histogenesis of striped muscle has been described by many workers, including Godlewski (2) (puppy, mouse, rat, guinea-pig), Bardeen (3) (pig), MacCallum (4) (pig, man), Schaffer (5) (various vertebrates); from these writers it is by no means clear whether the original myoblasts fuse to give rise to a syncytium, or whether each muscle cell arises from one myoblast that elongates with division of the nucleus (6). The development of cardiac muscle has been described by Retzer (7) (pig) and by MacCallum (8) (pig) and also by Tandler (11).

The present account is based on an investigation of human material only; it is incomplete in that the earliest embryo available was one of 10 mm., and also in that variations in the cardiac muscle of the different parts of the heart and the tracing out of the auricular-ventricular bundle (see Retzer (7) for pig) has not yet been done; it is hoped to make these points the subject of a later communication. The following is a description of the general appearances characteristic of various stages of development in the human: the interpretation of these appearances is not attempted.

The determination of the age of an early embryo is very difficult, the length of the embryo probably giving the best means of comparison: the ages given below have been determined during a systematic and comparative investigation of the general development of these embryos that Professor Lucas Keene and the writer are now engaged upon. The ages of older foetuses have been determined from the history, ossifications, and general post-mortem findings.

## (A) STRIPED MUSCLE

The voluntary muscle is developed from mesoderm which is early set aside for this purpose (9). In two human embryos of 10 mm. and 12 mm. respectively no differentiation of cells for this formation could be detected: in an embryo of 25 mm., however, among the branching general mesoderm cells could be seen quite clearly some elongated cells with long nuclei. These cells are found in the regions later occupied by the back muscles of the lumbar region, and represent the beginning of differentiation of mesoderm cells into striped

muscle cells. Even at this early stage the cells differ in size; this can best be seen in cross sections of the cells, the centre being occupied by either nucleus or non-staining protoplasm. The nuclei of these cells then begin to divide, and at *s[illegible] weeks* many cells show two nuclei and sometimes as many as four or five. The cells stand out from among the general connective tissue cells by virtue of their large amount of granular and strongly eosinophil cytoplasm.

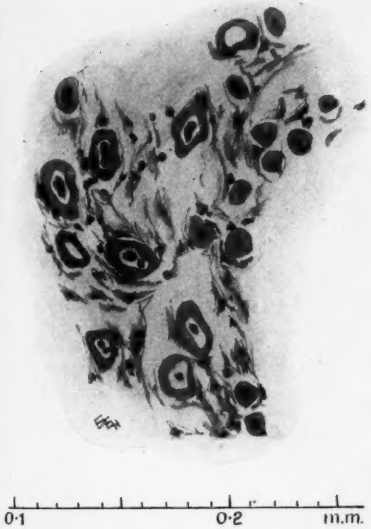


Fig. 1. Human embryo, aged about 7 weeks. Beginning of differentiation of striped muscle cells. Some cells already contain two nuclei and at this stage are nearly spherical.

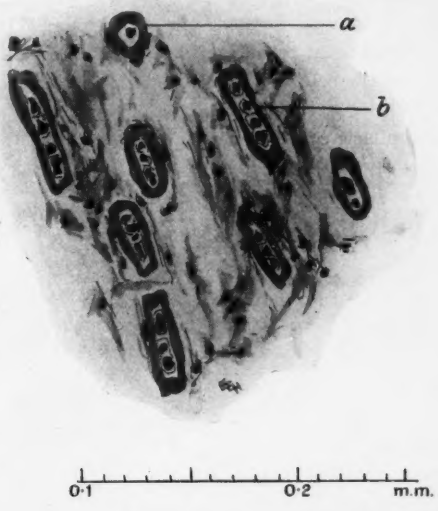


Fig. 2. Human embryo, aged about 8 weeks. Striped muscle cells further differentiated. Cross striations can be seen in some cells. Note central row of nuclei. The cells are in the region corresponding to fig. 1. *a*, cell in cross section; *b*, cell in longitudinal section.

At *eight weeks* (30–40 mm.) there is marked differentiation actually within these cells. The multinucleated cells have become larger, and the row of nuclei in the centre of the cell is embedded in a zone that does not stain but contains highly-refracting granules: outside this zone is the eosinophil cytoplasm that is now showing well-marked fibrillation in parts of the cells and also some cross striation. The cytoplasm which is being differentiated into contractile substance gives a curious staining reaction with Mallory's connective tissue stain: the nuclei are usually stained purple-red with an orange nucleolus, and the developing contracting substance either blue or orange or often mixed blue and orange. This possibly indicates a chemical modification, as fully differentiated muscle gives a uniform orange staining. The cells at this stage are said to be rich in glycogen.

As growth proceeds the fibrillation and cross striation gradually become more marked, and involve the whole fibre with the exception of the central row of nuclei with the surrounding undifferentiated protoplasm.

At *twenty-two weeks* the nuclei are taking up their permanent position. In a preparation from a foetus of this age some of the muscle fibres present an appearance very similar to that seen when fully developed, with nuclei beneath the sarcolemma, the cross sections of the fibres being however considerably smaller than they are at birth. Among these fibres, however, there are still to be found others of the embryonic type, with central nuclei surrounded by unstained undifferentiated protoplasm, showing fibrillation in the periphery of the cell only, very similar to the type of cell forming the Purkinje tissue of the heart. This embryonic type of fibre was not found among the striped muscle cells after the 26th week of foetal life.

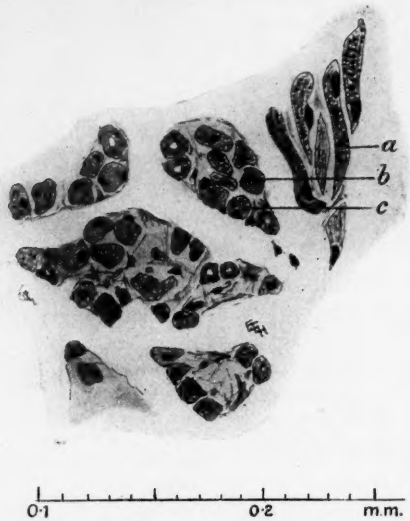


Fig. 3. Human embryo, aged about 22 weeks. Note nuclei of muscle cells either in the centre or at the periphery. The cells are in the region corresponding to fig. 1. *a*, cell in oblique section; *b*, cell in transverse section, with central nucleus; *c*, cell in transverse section, with peripheral nucleus.

At *full time* the striped muscle resembles exactly that of full development, except that the fibres are actually smaller. The variation in size of individual fibres as seen in cross section in the fully developed condition is present from the very beginning, as will be seen from the diagrams.

The developing muscle is richly supplied with blood vessels as early as six weeks. The ingrowth of nerve fibres has not as yet been studied in detail, but takes place at a very early stage of development. A delicate membrane is said

to appear about the 8th week, but a real sarcolemma is difficult to demonstrate. By a modified silver nitrate method, whereby the sarcolemma can be de-

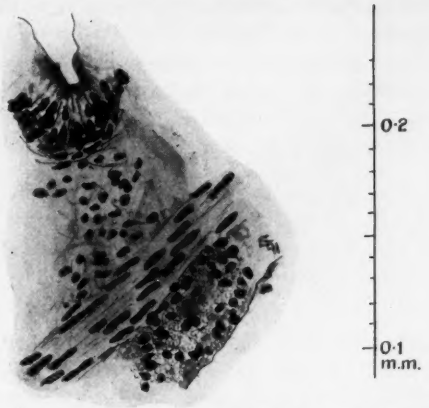


Fig. 4. Human embryo, aged about 7 weeks. Small intestine in cross section, showing unstriped muscle in transverse and in longitudinal section (compare fig. 5).

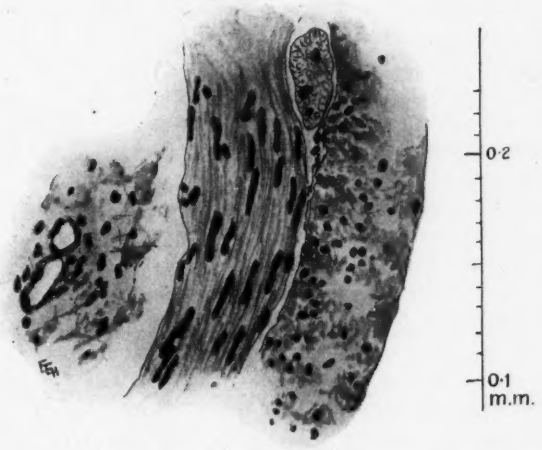


Fig. 5. Full-time human foetus. Unstriped muscle of small intestine. The growth of the cells is shown by the relative diminution in the number of nuclei.

monstrated in fully developed muscle, this structure has been distinguished in muscle from a foetus of 24 weeks.

MacCallum (4) notes the appearance of a single row of fibrils round the periphery of the cell in embryos of 75 mm. and 102 mm., and the nuclei nearly

all peripheral in embryos of 170 mm. At an early stage of development there is said to be a degeneration of some of the developing fibres, and a formation of new ones by longitudinal splitting of the remainder; this process was not observed in the preparations available.

The foregoing is an account of the development of the muscle cells in the lumbar region of the back: the muscle cells are formed in a similar way in other regions of the body.

### (B) UNSTRIPED MUSCLE

Unlike striped muscle, which arises from easily distinguishable cells that are early marked out for this purpose, unstriped muscle may arise from mesoderm cells in very various situations, and possibly also from ectoderm. These cells, which usually have an irregular and branching form and a round nucleus, elongate, and the nucleus becomes drawn out although remaining rounded at the poles. In an embryo of 10 mm. these were distinguished as long cells that were arranging themselves quite definitely round the lumen of the developing gut and of the larger blood vessels: the latter are extremely thin walled, and it is difficult to be certain whether these cells are actually developing muscle cells or only undifferentiated cells of the surrounding mesoderm. In a 12 mm. embryo these long cells with elongated nuclei can be found in almost all the situations where unstriped muscle will ultimately appear, being seen at this stage most clearly in the walls of the large blood vessels, of the alimentary tract, of the uterus and of the ureters. At *six weeks* these cells are lying parallel with one another, so forming definite sheets of muscular tissue in the walls of the various tubes. As development proceeds the cells acquire rather indefinite longitudinal striations and elongate to such extent that the number of nuclei seen in a given area of a section are less numerous (see diagrams).

The development of the unstriped muscle coats does not occur simultaneously in all the organs. Thus, at *eight weeks*, the longitudinal and oblique muscle fibres of the bladder wall are easily distinguishable but not the circular ones: in the gut the longitudinal muscle coat is more advanced in its stage of development than the circular coat in both small and large intestine, whereas in the oesophagus and in the stomach the muscle coats appear to develop at corresponding rates: the muscularis mucosae does not appear as a distinguishable layer until about 12 weeks. Again, at eight weeks the unstriped muscle of the trachea is well developed, but there is none in the bronchioles until about 11 weeks.

At *full time* the unstriped muscle resembles in appearance that of an adult, except that the cells are less elongated, and the nuclei more rounded, than they appear later.

### (C) CARDIAC MUSCLE

Although the heart itself is early differentiated yet the adult type of cardiac muscle is not developed for some time. In an embryo of 10 mm. the heart

tissue was found to consist of an open branching network of minute fibres, with many large round nuclei frequently showing mitosis. No striation could be detected in the fibres, and the appearance was that of a syncytium rather than that of definite cells. The same arrangement can be made out in slightly older embryos, and the appearance is that given by Tandler(11) for Keibel's Normentafel No. 27; at about *eight weeks* (or between 30 and 40 mm.) definite cross striations can be made out in some of the fibres. The nuclei are now spherical or ovoid, and lie in the faintly staining protoplasm in which are running many fibres. These fibres tend to run in groups parallel with one another, the individuals running first with one group and then breaking away to join an adjacent group. The nuclei in some cases appear somewhat elongated as if pressed among the fibres, but more frequently they lie in more open spaces between the groups. As differentiation proceeds the fibres become more strongly eosinophil. At first sight one might think that the fibres really represent cell boundaries, but a careful examination of the relation between the nuclei and the fibres as seen in transverse and longitudinal section shows that some at least of the fibres are of far greater length than would correspond to the cells. (Mallory's connective tissue stain after formalin fixation brings out these features more clearly than any other method tried.)

By 11 *weeks* development of a few transverse "cell boundaries" can be seen. The fibres, in which striation is more clearly seen than at ten weeks but is still far from universal, run parallel with each other, and arrange themselves loosely in groups, any one fibre attaching itself to several groups in succession. The nucleus is often surrounded by faintly staining undifferentiated protoplasm which appears continuous with that between the fibres. The whole tissue is very richly supplied with capillary vessels.

As development proceeds the cross striated fibres become more general, but the nuclei still retain the surrounding zone of undifferentiated protoplasm. The fibres gradually become more closely packed together, and the nuclei become rather more drawn out and elongated. At 16 *weeks* the cross striations are further apart than they are a few weeks later, and are not yet present in all the fibres.

By 20 *weeks* the continuity of the fibres for comparatively long distances can be clearly seen, but the transverse cell boundaries are still rare; the cross striation of the fibres has now become universal.

The individual fibres gradually increase in thickness, and the nuclei tend to become more elongated, and thus the fully developed type is finally reached. The nucleus often retains a small surrounding zone of undifferentiated protoplasm, and a general appearance of "cells" may be given by the way in which the fibres arrange themselves in groups, and by the so-called cross "cell boundaries"; according to Krause(10) these latter are to be regarded as of the nature of discs interpolated on the course of a bundle of fibres. The yellow pigment frequently associated with the nucleus in later life has not been seen in foetal material.

## CONCLUSIONS

In the human foetus it was found that of the three types of muscle the unstriped is the first to develop, being clearly defined in an embryo of 10 mm., and is also the one that shows the least subsequent differentiation. The striped muscle begins to differentiate at about 25 mm., but the development is slow and the adult type is not found until about 22 weeks. The cardiac muscle is differentiated probably before 10 mm., but striations were not clearly seen until between 30 and 40 mm. (eight weeks).

This special piece of work was undertaken during the course of an investigation on the human foetus that is being carried out jointly with Professor M. F. Lucas Keene, and for which we beg to acknowledge a grant from the Thomas Smythe Hughes Medical Research Fund of the University of London. I also have to thank the Medical Research Council for a grant.

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# FOUR CASES OF FOURTH MOLAR TEETH IN SOUTH AFRICAN BABOONS

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## INTRODUCTION

During the past year there has been in progress in this Department an extended study of the skeletal features of South African baboons.

The primary object of the investigations undertaken has been the elucidation of the relation to modern baboons of the fossilised baboons found at Taungs, Bechuanaland. The recovery of these cercopithecid fossils has revealed the inadequacy of our knowledge of the detailed anatomy of the cranial forms of living baboons.

Professor Raymond A. Dart has therefore had gathered together in his Department a considerable number of baboon skulls of different ages and sex and this collection has been supplemented by the rich collections of the Museums of Albany and Pretoria, secured through the generosity of the Directors and Trustees.

In another place Mr I. Goldblatt (1926) has made a critical survey of the cranial form of the so-called Cape and Transvaal baboons. It is my object to set on record in due course the results of a detailed examination of the teeth in South African varieties of baboons. During the course of this investigation it has been my fortune to encounter a number of skulls presenting anomalous conditions of the molar teeth. This was not expected, for Duckworth (1915) has stated that "accessory molar teeth are very infrequently found in the Cercopithecidae."

These anomalies of dentition have appeared to me, on account of the stated rarity, to be of sufficient interest to warrant a special report concerning them.

## THE MATERIAL

The material used during the course of the investigation consisted of one hundred and twelve skulls of South African baboons. The dentitions of four of these form the especial subject of the present report.

Sixty of the skulls are the property of the Museum of Albany, thirty-nine are the property of the Museum of Pretoria and the remainder form a part of the collection in the Anatomical Museum of the University of Witwatersrand, Johannesburg[1].

## PRESENT OBSERVATIONS

Among the skulls examined four presented the anomaly of either a fourth molar tooth or a well-formed alveolus which testified to the presence of a fourth molar tooth during life. Ten others gave evidence, through "Dellen" or fossae, of the previous existence of fourth molar rudiments at some earlier stage of development.

The dentitions of these crania will now be described in detail.

### *Cranium number* 757 (*Pretoria Museum*)

This cranium is most remarkable in exhibiting supernumerary teeth in both sides of both upper and lower jaws.

*Upper jaw.* The dental arcade was originally complete but a few teeth are now absent from the dry specimen. The first molar teeth show signs of considerable wear, indicating that the animal was a fairly old adult. Fourth molar teeth are present in the right and left sides, distal to the third molar teeth (Plate I, fig. 1). They are smaller than the third molars in their mesio-distal length. Their occlusal surfaces are small in comparison to the corresponding surfaces of the other molar teeth. Only about one-sixth of their crowns remains to be erupted and exposed in the dental arcades. Their mesial cusps are better developed than their distal cusps and the bucco-lingual diameters of their crowns are greater on the mesial than on the distal surfaces. Notwithstanding these features, the supernumerary teeth are well formed; they have each four cusps and three normally developed roots which are firmly implanted in their sockets.

*Lower jaw* (*vide* Plate I, fig. 2). The mandibular dental arcade is complete except for the left first premolar, most of which was lost during life. Fourth molar teeth are present on both sides in this jaw also and they are in an infinitesimal degree less erupted than the corresponding teeth in the upper jaw. Their

[1] I wish here personally to express my gratitude to the Directors and Trustees of Albany and Pretoria Museums for their courtesy in lending their valuable collections to this Department. I also wish to express my gratitude to Professor Dart for his permission to make use of the skulls in the Museum of Anatomy, and also for his assistance and criticisms afforded during the investigation.

occlusal surfaces are on a much lower plane than that of the molar teeth in front of them. This is in part due to an inclination of their crowns towards the mouth cavity. Well formed in all other respects, these additional teeth resemble typical third lower molars and except for the absence of a slight degree of wear they are virtually identical with the third molar teeth present.

*Measurements.* The mesio-distal length of the first three maxillary molars equals 39·5 and 38·5 mm. on the right and left sides respectively.

The fourth maxillary molars have a mesio-distal length of 12·5 mm. and a bucco-lingual width of 10·0 mm. They are shorter mesio-distally than the second and third molars (which measure 13·5 mm.) and longer than the first molars (which measure 11·5 mm.). Bucco-lingually they are the same width as the third molars, ·5 mm. narrower than the second molars and 1·0 mm. wider than the first molars.

The mandibular third and fourth molars measure 16·0 mm. mesio-distally and 10·5 mm. bucco-lingually. The other molar teeth are of relatively normal size.

### *Cranium H (Pretoria Museum)*

The mandibular and maxillary dentitions are complete and normal except for the presence of an unerupted fourth molar tooth in the maxillary alveolus on the right side (Plate I, fig. 3).

*Upper jaw.* The occlusal surface of the supernumerary molar is about 12·0 mm. below the occlusal surface of the neighbouring third molar, but absorption and injury to the overlying bone permit a clear view of the general form and shape of its crown surface.

Four cusps are present of which the mesial ones are the better developed. The occlusal surface is small but normal in its relation to the size of the crown.

On the left side of the maxilla, distal to the third molar, there is a triangular depression or fossa which will be described later.

### *Cranium number* 48 *(Albany Museum)*

In this specimen also the dental arcades are complete. A supernumerary tooth is present in the right maxillary alveolus (Plate I, fig. 4).

*Upper jaw.* The additional molar is not as fully erupted as those in skull 757. It has four cusps of which the two on the buccal side are well formed and normal. The two on the lingual side are not so well formed and are joined together at their base. The roots are two in number, one mesial and one distal. The mesial root is deeply grooved on its distal aspect and shows a tendency towards the formation of a mesio-lingual root.

As in skull H, there is a triangular fossa in the left maxillary alveolus.

*Measurements.* The mesio-distal length of the first three maxillary molars is 40·0 mm. on both the right and left sides.

The fourth molar tooth has a mesio-distal length of 14·0 mm. and a bucco-lingual width of 12·0 mm. The former measurement is ·5 mm. less than the mesio-distal length of the third molar and is similar to that of the second molar. The latter measurement is 1·0 mm. less than the bucco-lingual width of the third molar and is again similar to that of the second. The first molars are relatively normal in size.

*Cranium number* 46 (*Albany Museum*)

The fourth molar tooth has been lost post-mortem in this skull but the condition of the alveolus on the right side of the maxilla distal to the third molar testifies to the loss of a tooth which was present in this position during life (Plate I, fig. 5). The tooth had been fully erupted and possessed two roots. It was evidently also a smaller tooth than any of the molar teeth present. In addition to the supernumerary tooth, several other teeth have been lost post-mortem.

*Measurements.* The mesio-distal length from the first to the third molars is 40·0 mm. on both the right and left sides.

*The Fossae.* The presence of triangular fossae, distal to the third molar teeth, have already been noted when dealing with skulls 48 and H.

These fossae are precisely similar to and are apparently homologous with the fossae or "Dellen" described by Zuckerkandl in human crania. In the chimpanzee similar fossae were noted by Selenka but he apparently failed to recognise their morphological significance as homologous with human "Dellen." So far as I am aware, this is the first recognition of "Dellen" in primates other than man and the great apes. Their presence was noted in ten additional specimens of baboons of this series, i.e. they occur in 12 per cent. of cases.

Zuckerkandl regarded them as evidence of the existence of rudimentary alveoli at some earlier stage of development. By their general form, shape and position this view is ratified in the skulls here described.

In no instance were they present in the lower jaw. In five cases they were present on both sides in the upper jaw, immediately distal to the third molars.

## FOURTH MOLAR TEETH IN OTHER PRIMATES

*In the Hominidae.* From the available records it appears that additions to the molar series in this group of the primates are usually fourth molar teeth. Fourth molar teeth have been recorded in many Europeans, Asiatics, African and Australian natives, but, according to Duckworth (1915), "such anomalies are more frequent in the Melanesian and Australian Aborigines than in any other Hominidae." Campbell (1925) informs us that the abnormality occurs in 1·5 per cent. of the Aboriginal Australians. At the Dental Clinic of the Witwatersrand University I have noted frequently the presence of fourth molar teeth in native patients but at present sufficient data is not available to estimate the percentage of cases in which the anomaly occurs.

*In the Anthropoid Apes.* The apes provide the largest number of examples of the fourth molar condition and among them the orang-utan provides more examples than either the gorilla or chimpanzee which come next in sequence.

According to Selenka (1899), fourth molar teeth are present in 20 per cent. of adult orang-utans and in about 8 per cent. of adult gorillas. In the chimpanzee this writer found but one instance of an accessory molar but he states that there was evidence of a tendency towards the development of such in a larger number of cases. (This evidence was presumably the fossae or "Dellen" already referred to.)

Bateson (1892) records having examined thirty-five skulls of the chimpanzee and found either fourth molars or their empty sockets in four cases.

Duckworth (1915) is in agreement with Selenka as to the frequency of occurrence of the condition in the gorilla but "after an examination of 200 crania at Munich" he places the corresponding percentage for the orang-utan at 15 per cent.

The Hylobatidae, among the Simidae, appear to have provided very few examples of the fourth molar anomaly. Duckworth (1915) failed to find a solitary example in a collection of fifty crania.

*In the Cercopithecidae.* It has been shown in this paper that accessory molar teeth occur in one genus of Cercopithecidae in about 4 per cent. of cases and that there is evidence of a tendency towards the occurrence of such in 12 per cent. of cases. The condition is said to be rare in the other genera of the family.

*In Cebidae, Lemuridae and Hapalidae.* The available literature is not sufficient to summarise the occurrence of the anomaly in these families. In fossil and modern lemurs the anomaly has been recorded on more than one occasion. According to Duckworth, "the genus Ateles among the Cebidae furnishes more examples than either the genera Mycetes or Cebus."

## THE SIGNIFICANCE OF THE FOURTH MOLAR

At least three theories have been advanced in explanation of the fourth molar condition. These are:

1. Bolk's Theory.
2. The Inheritance Theory.
3. Gregory's Theory.

1. *Bolk's Theory.* According to this theory, fourth molar teeth should be regarded as "Reversions" to a three molar type of dentition.

Professor Bolk considers that there are no third permanent molar teeth in modern primates. He postulates that the teeth so-called are second permanent molars, that the second permanent molars are first permanent molars and that the first permanent molars are homologous with the third deciduous molars of Platyrrhine primates.

These assumptions form the basis of his theory.

The theory has been adequately discussed and condemned by Gregory in his book—*The Evolution of the Human Dentition.* The writer has here nothing further to add concerning it.

2. *The Inheritance Theory.* The inheritance theory is based on the assumption that the "ancestors of the primates" had four molar teeth on each side of each jaw as the normal number. Fourth molar teeth are regarded by advocates of the theory as "Reversions" to the four molar type.

3. *Gregory's Theory.* Gregory considers that "the presence of a fourth molar tooth in modern mammals may be ascribed to a specialised and relatively new tendency of the dental lamina to bud off more than the normal number of teeth...the fourth molar when present is in all probability a neomorph both in man and the anthropoidea."

## THE WRITER'S VIEW

The writer considers that a combination of Gregory's theory and the inheritance theory will give a better explanation of the fourth molar anomaly than will either of the theories by themselves.

An additional factor, one not considered in either of these theories, is believed however to be concerned also in determining the presence of the additional tooth. This factor is "Alveolar Prolongation."

Early in this investigation it was noted that wherever a fourth molar tooth was present the alveolus appeared to be prolonged backwards. To determine whether this alveolar prolongation determined the presence of the fourth molar or *vice-versa,* measurements were taken.

In 98 normal skulls the centimetre-long average prolongation of the tuber maxilla was 1·97 cm. In 14 skulls which possessed either fourth molars or "Dellen" it was 1·90 cm.

Thus the results obtained indicated that the additional tooth was largely conditioned by exuberant alveolar growth.

Many years ago (1905) Wilson arrived at a similar conclusion when investigating the fourth molar anomaly in the aboriginal Australians.

The writer therefore believes that inheritance, alveolar prolongation, and a new tendency of the dental lamina to bud off more than the normal number of teeth, are the factors responsible for the production of fourth molar teeth. It would not appear possible to determine which factor, if any, plays the major part. Further knowledge of the actual embryonal causes which determine the first rudiments of any tooth is essential for the solution of this problem.

## CONCLUSIONS

1. Fourth molar teeth are the result of hereditary influences, alveolar prolongation, and a new tendency of the dental lamina to bud off more than the normal number of teeth.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

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2. Fourth molar teeth occur in about 4 per cent. of adult South African baboons or if fourth molar dental rudiments be included 14 per cent.

3. Male baboons provide the majority of recorded cases.

4. In the baboon the anomaly occurs more frequently in the upper than in the lower jaw.

5. Where only one fourth molar tooth is present, it is usually in the right side of the maxilla.

## EXPLANATION OF PLATE

Fig. 1. Cranium number 757 (Pretoria Museum). Note the fourth molar teeth in the right and left sides of the maxillary alveolus.

Fig. 2. Cranium number 757 (Pretoria Museum). Note the fourth molar teeth in the right and left sides of the mandibular alveolus.

Fig. 3. Cranium H (Pretoria Museum). Note the partially erupted fourth molar tooth in the right maxillary alveolus.

Fig. 4. Cranium number 48 (Albany Museum). Note the unerupted fourth molar tooth in the right maxillary alveolus.

Fig. 5. Cranium number 46 (Albany Museum). Note the condition of the alveolus on the right side of the jaw, distal to the third molar.

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# AN UNCOMMON ABNORMALITY OF THE FLEXOR DIGITORUM SUBLIMIS MUSCLE

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The abnormality here described was discovered recently in the routine dissection of the body of a very muscular man, found drowned, aged apparently about forty-five, but of unknown name and occupation.

In the left superior extremity the flexor digitorum sublimis arose in quite the customary manner, the deeper portion of the muscle possessing a fleshy origin from the anterior aspect of the medial epicondyle of the humerus, the anterior band of the ulnar collateral ligament of the elbow joint, and the medial margin of the coronoid process of the ulna. About 5 cm. distal to the coronoid process, tendinous fibres appeared on the posterior aspect of this fleshy mass, and then the whole radial part of the deep layer of the muscle became a rounded tendon (*T* 1), from which arose fleshy fibres contributing to the tendons for the ring and little fingers. At the junction of the middle and distal thirds of the forearm arose a muscular belly (*B* 1), giving rise at its distal end to a tendon (*T* 2). To the radial and posterior part of the belly was attached the now somewhat flattened tendon (*T* 1), which, 2 cm. distal to the proximal end of the mass (*B* 1), expanded into a second mass (*B* 2), attached not only to its tendon of origin (*T* 1), but also to the posterior aspect of the proximal part of the belly (*B* 1), the fibres of the two being closely adherent and parallel. The second lay partly behind and partly radial to the distal and radial portion of the first belly, and then on the radial side of the tendon of the latter (*T* 2). Immediately proximal to the wrist a tendon (*T* 3) arose on the antero-ulnar aspect of *B* 2, and this tendon joined the postero-radial margin of *T* 2 opposite the distal part of the carpus, forming a tendon (*T* 4), which was inserted into the index in the normal manner. Fleshy fibres were, however, prolonged distally, adherent to the posterior, radial, and to a

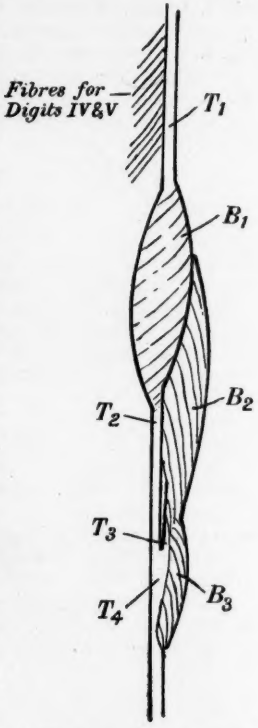


Diagram of the supernumerary muscle bellies and tendons.

considerable extent, to the anterior aspects of *T* 3, and to the radial and anterior aspects of *T* 4 for its proximal 2·5 cm., these fibres forming a belly (*B* 3), which ended abruptly on the tendon (*T* 4) at about the level of the first metacarpo-phalangeal joint. *B* 1 and *B* 2 lay in a plane posterior to the parts of the flexor sublimis for the middle and ring fingers, these parts causing depressions on the bellies (*B* 2 and *B* 1 respectively).

The following are approximate sizes of the parts described:

*B* 1: 6 cm. long; 2 cm. antero-posteriorly; 1·5 cm. from side to side.

*B* 2: 6 cm. long; 1·3 cm. antero-posteriorly; 1 cm. from side to side.

*B* 3: 4·5 cm. long; 0·8 cm. antero-posteriorly; 0·5 cm. from side to side.

*T* 2: 4 cm. long; 0·3 cm. in diameter.

*T* 3: 2 cm. long; 0·3 cm. in diameter.

*T* 2, *T* 3 and *B* 3 passed deep to the transverse carpal ligament. The dissectors had not noticed whether there was an attachment of that ligament to any part described, but there were no traces of the ligament such as are often left on the palmaris longus after dissection. No nerve supply was left. No other outstanding abnormality was present, but the following points were noted:

(1) The very small size of the ulnar head of the pronator teres.

(2) The absence of the palmaris longus.

(3) The subdivision of the flexor digitorum profundus into its four digital portions in the proximal third of the forearm.

(4) The large size of the arteria mediana, which provided the digital arteries for the cleft between the index and middle fingers.

(5) The perfectly normal development of the four lumbrical muscles.

On the right side there were no muscular abnormalities; the palmaris longus was present; the median artery was similar to that of the left. The greater volume of the muscles of the left side suggested left-handedness.

In spite of a careful review of the accessible literature, I have been unable to discover either a description of, or a reference to, an exactly similar abnormality. Fleshy fibres connected with the tendons of the flexor digitorum sublimis in the palm, and either replacing the lumbricals or constituting accessory lumbricals, have been described by various writers, as mentioned by Le Double (1897). More recent is the accessory lumbrical of the index described by Cordier (1920). In Fromont's (1895) case, besides the replacement of the sublimis tendons for the left index and little fingers by muscular fibres lying deep to the palmar aponeurosis and attached proximally to the transverse carpal ligament, the existing sublimis tendons to the middle and ring fingers received the insertion of similar fleshy slips. The right side showed a somewhat similar arrangement. Of special interest is the occurrence described by Gräper (1917) of the interruption of the index sublimis tendon by a fleshy belly lying in the hand.

The scheme of development of the forearm and hand musculature at present most generally accepted is that based on the phylogenetic evidence of Eisler (1895) and McMurrich (1903, *a* and *b*) and on the ontogenetic

evidence of, for example, Gräfenberg (1906). For the present purpose it will be sufficient to mention that the human flexor digitorum sublimis is supposed to be developed in part from the primitive flexor mass of the forearm and in part from the short superficial flexors of the digits. These latter lie between the two layers into which the primitive palmar aponeurosis has divided, and are attached to the deep surface of the more superficial of the layers (i.e. to the definitive aponeurosis). The fleshy fibres become mainly tendinous and detached from the aponeurosis. This scheme provides a considerable part of the explanation of anomalies such as those quoted above, and, as Eisler (1895) pointed out, provides the most satisfactory reason for the digastric condition of the sublimis. This condition is most clearly seen in the portion of the muscle supplying the index, and one may without hesitation suppose that the bellies (*B* 1) and (*B* 2) of the case described are wholly or partly the more distal of the two bellies of the normal digastric muscle, that is, are wholly or partly derived from the short superficial flexor of the index. The belly (*B* 3) appears to be a part of the same muscle here unconverted into tendon, a lesser degree of regression than in Gräper's case (1917). There seems to be no reason to suppose that it has any connection with the development of lumbricals.

To account for the occurrence of the two forearm bellies, several suggestions occur:

(1) Migration distally of an accessory coronoid head of the deeper stratum of the sublimis. Against this is the obvious fleshy continuity of the parts (*B* 1) and (*B* 2) with (*B* 3).

(2) Appropriation by the index of a part of the primitive short flexor normally incorporated in a neighbouring sublimis tendon, or of fibres normally incorporated in the profundus. In so far as the existing volumes of the parts concerned form satisfactory evidence, they oppose the suggestion.

(3) Division, at an early stage of development, of the superficial short flexor of the index, as suggested by Congdon (1920) to account both for the abnormal occurrence in man of short flexor remnants along with sublimis tendons, and also for the normal occurrence of short as well as long superficial flexors in certain animals, e.g. those mentioned by Kajava (1911): certain Carnivores, Insectivores, and the isolated ungulate genus—*Hyrax*. A similar process seems to be indicated by Backman (1925) in an attempt to account for more extensive reduplications—a process of fission in the pre-muscle mass. The present instance therefore suggests a separation of the superficial flexor brevis into a volar and ulnar part (*B* 1 with *T* 2), corresponding to the fleshy slips in Fromont's case (1895), and a dorsal and radial portion (*B* 2 with *T* 3 and *B* 3), corresponding in Fromont's case to the sublimis tendons where these were present. (Unfortunately the destruction of the forearm prevented Fromont ascertaining the disposition of the sublimis proximal to the wrist.) The large volume of the parts here is doubtless explicable on functional grounds.

While the persistence of fleshy fibres on the sublimis tendon in the palm is looked upon as a regressive variation, the rarity of reduplication of flexors

in that region disfavours, as Congdon pointed out (1920), the possibility of an ancestry in which short and long superficial digital flexors coexisted, and one must for the present classify the reduplication as a "fortuitous" variation. A point of special interest is, that this reduplication has extended in this instance into the forearm.

## SUMMARY

The case is one in which the index portion of the left flexor digitorum sublimis of an adult male formed two bellies with separate tendons in the distal third of the forearm, and a further smaller belly in the palm.

The current view of the development of the muscle concerned is recalled, and it appears that, while the presence of the fleshy fibres in the palm indicates persistence of part of the short superficial digital flexor, the reduplication is probably to be looked upon as a "fortuitous" variation due to fission of the index portion of the short flexor at an early stage of development.

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# A "POST-ORBITAL" BONE IN THE BABOON *PAPIO PORCARIUS*

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## INTRODUCTION

During the course of an investigation into the cranial characters of the baboon *Papio porcarius* in this country, it was noticed that certain of the skulls of these baboons exhibited an anomalous bone situated on the zygomatic arch close to, or at, the sutural junction of the zygomatic process of the temporal bone with the temporal process of the zygomatic bone (fig. 1). No attention was paid to this abnormality at that time, but later Prof. Dart pointed out that it was unique in his experience, and a study of the literature available provided no reference to such an anomaly in man or the primates. It was therefore decided that an account of the anomaly and some discussion of its apparent significance was desirable.

## MATERIAL

The baboon skulls examined consisted of the following specimens:

*From the Cape Province:* 5 males, 4 females, 2 infants from Phillipstown; 2 males from Queenstown; 2 males from Knysna; 1 male from Paarl; 3 males from Ceres; 48 males, 3 females, 2 infants from Albany; 1 male from Uitenhage; 1 male from Alicedale; 1 male from Fort Beufort. Total 75.

*From Transvaal:* 4 males, 1 female from Rustenberg; 1 male from Magaliesberg; 1 male from Komatipoort; 1 male from Hekpoort; 1 female from Pietersburg; 1 male from Lekkerkraal; 2 males from Waterberg District; and 4 males, 4 females, 3 infants—the precise locality from which they were obtained in the Transvaal being unknown. Total 23.

This material formed the subject matter of a paper published in the *South African Journal of Science* (1926) and as stated there consisted of the collections of this Anatomical Department together with those of the Transvaal and Albany Museums. I beg to acknowledge the generosity of the Directors of the aforesaid Anatomical Department and Museums.

## THE ANOMALY

Fig. 1 is a dioptographic tracing of the right zygomatic arch region of three baboons called by me (1926) *Papio porcarius orientalis*. It depicts three striking varieties of the anomaly (*P.O.*) in question. This abnormality occurs either on the right or left side but never, in my experience, on both sides in one and the same specimen. It is present in my specimens only in adult males. Its size, shape and position vary. In some it is represented by a small tubercle, triangular in shape, and being about 4 mm. in its greatest dimension; in others it is larger, measuring as much as 23 mm. by 8 mm. and is rectangular (fig. 1, *A* and *C*). The bone under discussion forms in some instances a wedge inserted at the upper part of the tempero-zygomatic suture between the two bones entering into the constitution of the zygomatic arch (fig. 1, *A* and *B*); in others it occurs on the upper border of the zygomatic process of the temporal bone, just posterior to the suture (fig. 1, *C*). The bone is usually clearly demarcated from the bone or bones next to it by one or two sutures, but in some cases it seems to be continuous with either the temporal or the zygomatic or with both bones. Its presence was detected in 16 out of 79 adult male specimens (20 per cent.). It is interesting to note that it occurred in 15 of 64 specimens (25 per cent.) of *Papio porcarius orientalis*, and in 1 of 15 specimens (6·7 per cent.) of the sub-species *Papio porcarius occidentalis*, recently

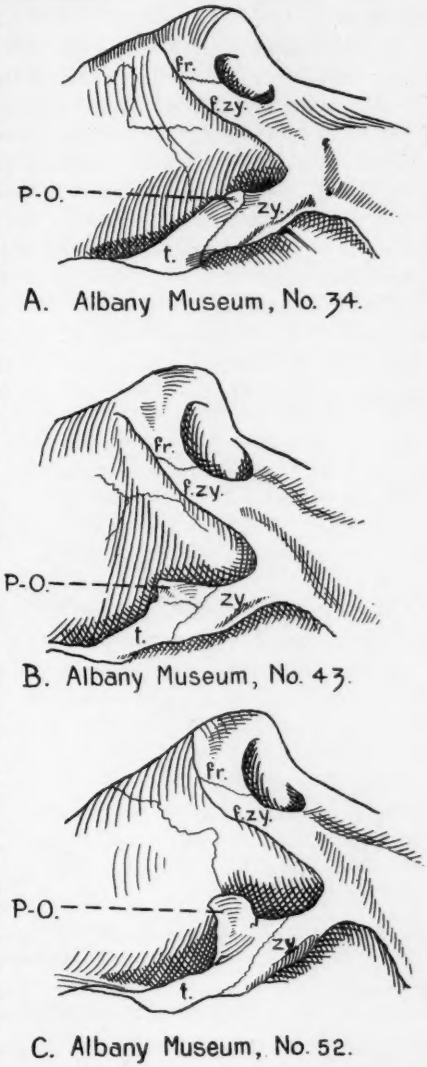


Fig. 1. Three examples of the "post-orbital" anomaly (*P.O.*) in *Papio porcarius orientalis*. *fr.* = frontal; *f.zy.* = frontal process of zygomatic (jugal); *zy.* = temporal process of zygomatic (jugal); *t.* = zygomatic process of temporal (squamosal).

described by me (*loc. cit.* 1926). Furthermore, in the case of the former all the abnormal specimens were obtained from Mountain Top, Albany, Cape Province.

(In the paper by me above referred to, I pointed out that there exist many well-defined differences between the skulls of the baboons (*orientalis* inhabiting the eastern regions of the Transvaal and Cape Province and those (*occidentalis*) inhabiting the western areas of these two provinces. Thus the oriental forms have a smaller spheno-maxillary angle, and are therefore less prognathic than the occidental. The total length of the skull, muzzle and brain case is greater in the eastern than in the western baboons, and the latter have a larger cranial volume than the former. In order to illustrate graphically some of these differences in this paper, fig. 2 is here inserted. On the basis of these and other points of difference I divided the South African baboons into two sub-species, *P. porcarius orientalis* inhabiting eastern Transvaal and Cape Province and *P. porcarius occidentalis* inhabiting the western portions of these two provinces.)

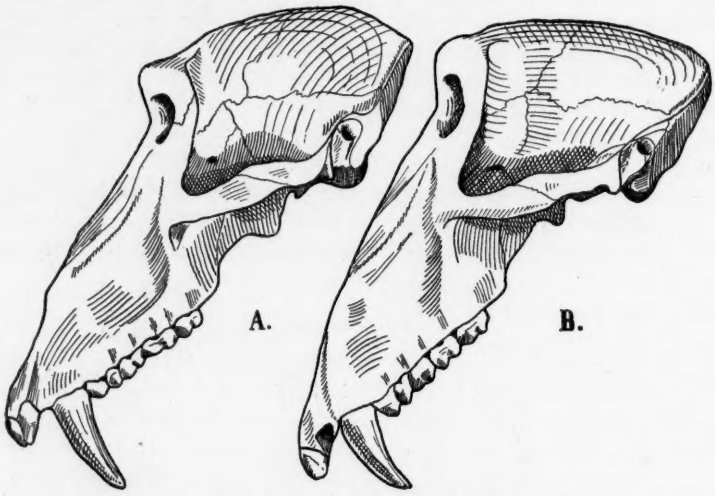


Fig. 2. *A* = *Papio porcarius occidentalis*; *B* = *Papio porcarius orientalis*. The two types of South African baboon drawn on the same horizontal plane

## THE SIGNIFICANCE OF THE ANOMALY

Careful examination of the abnormal piece of bone and of the area around shows that it is not pathological in nature. There is no evidence that any inflammatory reaction occurred at the site. The bone is regular and smooth and corresponds in every detail with normal, healthy membrane bone. Furthermore, as already stated, it is in some cases distinctly separated from the surrounding bone by a suture. The skulls were also referred to

Dr A. S. Strachan, Head of the Department of Pathology in the University of the Witwatersrand, for opinion, and, after examining them, he stated that he could find nothing which would indicate that the bone was pathological.

The fact that the bone under discussion is in some instances separated from the bones around it indicates also that it cannot be a hypertrophic or hyperplastic manifestation, such as one would suppose might occur if the masseter muscle underwent a process of hyperplasia and then needed additional bone for its attachments. The abnormal bone occurs on one side only, and, except for its presence, the zygomatic arch is of exactly the same size and strength on both sides. This would show that the postulated hyperplasia must have occurred on one side only, which seems improbable. In any case the mandibles show no evidence of hypertrophy in any feature. Finally, the bone in question, being placed on the superior border of the zygomatic arch, was not related to any muscle, but was continuous with the temporal fascia, and it is hardly likely that the fascia would evoke such an increase in the amount of bone in the arch.

Seeing then, that there is no evidence of pathological abnormality nor of hyperplasia due to increased functional demands, one is justified in concluding that the bone in question is the result of an excess in the processes of development. According to the literature consulted, there is some diversity of opinion on the subject of the ossification of the membrane bones of the skull. Some authors (Keibel and Mall, 1912; Keith, 1921; Prentiss and Arey, 1918; Arthur Thomson, 1924) hold that in the human skull the zygomatic bone, including its temporal process, and the squamous temporal, with its zygomatic process, are each ossified in membrane from a single centre. These observers are also agreed that in some cases the zygomatic is ossified from two centres which may fail to unite and so leave the bone in a divided condition (i.e. os japonicum). Other investigators (see Minot, 1897; F. Frassetto, 1913; Oskar Hertwig, 1906) claim that the zygomatic and squamous temporal bones are each ossified from three centres. None of these, however, appear actually in the zygomatic process of the temporal bone or in the temporal process of the zygomatic bone. In the baboon skulls with abnormal zygomatic arches it is certain, in some cases at any rate, that a separate centre of ossification appeared in the membrane between the regions where the zygomatic process of the temporal bone and the temporal process of the zygomatic bone were developed, and that by this separate centre of ossification the anomalous bone was formed.

The recognition of a separate bony element in this region suggested naturally a detailed examination of all the human and other primate skulls in the department for the occurrence of some remnant, vestigial or otherwise, of it in the normal skull.

In a few baboon skulls, mostly young specimens, the superior border of the arch forms a perfectly straight line, but in the vast majority of cases (85 per cent.) there appears on this border, just posterior to the temporo-

zygomatic suture, a rounded prominence, convex superiorly (fig. 2). In these cases, therefore, the superior border of the arch is, in its anterior one-third, straight and, in its middle one-third, convex superiorly. The prominence is, of course, on the zygomatic process of the temporal bone, and it is important to note that, when the anomalous bone is related to the temporal bone only, it appears in the position normally occupied by the prominence in question (fig. 1, *C*). This would indicate that the formation of the anomalous bone is due to the exaggerated activity of the processes which normally produce the prominence only. The prominence becomes increasingly evident with age, but there is nothing to show, save in the special cases already referred to, that it increases in size relative to the whole zygomatic arch. In other words the prominence is indicated even in the infantile arch.

Such a prominence we found also in many other primate skulls—some human skulls, gorilla skulls, where it is well marked, in an old female chimpanzee (but not in four young specimens at the stage of the eruption of the first permanent molar), in *Macacus cynomolgus*, *Hylobates syndactylus*, and in the baboons *Cynocephalus hamadryas* and *Papio cynocephalus*.

It would therefore appear that the occurrence of a bony prominence in this region is a common occurrence in most old-world primate skulls, but the occurrence of a separate bone in this area is very unusual except in the case of the eastern variety of the South African baboon.

Prof. Dart pointed out to me that there is present on the medial aspect of the zygomatic arch in some human skulls a ridge of bone running upwards and backwards on the zygomatic process of the temporal bone, from the lower end of the temporo-zygomatic suture to a point on the inner aspect of the superior border of the arch, about 1 cm. behind the suture. He suggested that this ridge might have some significance in view of the phylogenetic processes which have taken place in this region, and that the portion of bone between the ridge in question and the suture might represent the homologue of the anomalous bone here being considered.

The frequency of the occurrence of this ridge in the skulls of the various human races at our disposal has been determined and the following table indicates the occurrence of both the ridge and the prominence above referred to in the skulls of three human races in South Africa.

| Race | No. investigated | Ridge | Prominence |
|---|---|---|---|
| European | 18 | 4 | 10 |
| Negro (unclassified) | 32 | 6 | 11 |
| Bush | 6 | 0 | 0 |
| Totals | 56 | 10 | 21 |

From what has been said, it is clear that the anomalous bone we are here dealing with is the result of an excess in the processes of development, and the question now arises whether this excess in ontogeny has a phylogenetic significance.

Most modern zoologists are agreed that the ancestral pro-mammalian form was reptilian. If we examine the skulls of the so-called mammal-like reptiles, those grouped in the sub-class Theromorpha, we find a type of zygomatic arch of which the abnormal ones in our baboon skulls are strangely reminiscent. Figs. 3 and 4 show diagrammatically the cranial structure in four different genera of Theromorpha. It will be seen that one of the outstanding features in these skulls, and one which illustrates their resemblance to the mammalian type is the zygomatic arch. This structure in the Theromorpha is composed essentially of the squamosal (temporal of mammals) and the jugal (zygomatic of mammals) bones, but the post-orbital bone, e.g. in *Placochelys*, or the post-frontal bone, e.g. in *Dicynodon*, also enter into its formation. The presence of this separate bone is the essential difference between these Theromorpha and the mammalian zygomatic arches.

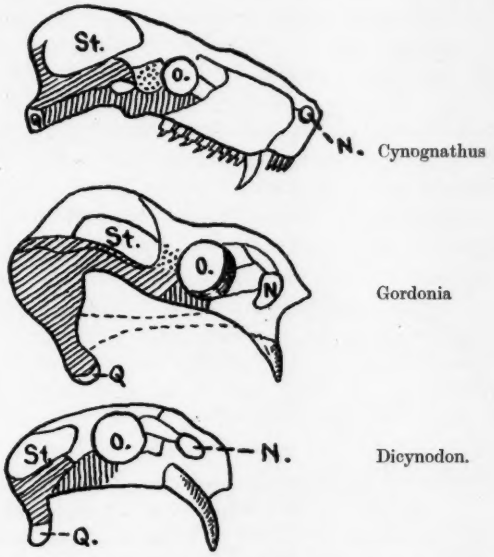


Fig. 3. Three generic types of Theromorph reptiles showing composition of bony arches of orbito temporal region of the skull. (After Gadow, *Camb. Nat. Hist.* vol. VIII.)

Vertical shading = jugal. *O.* = orbit.
Oblique shading = squamosal. *N.* = nasal groove.
Dotted = post-orbital. *Q.* = quadrate.
*St.* = supratemporal fosso.

If we examine the post-orbital bone more closely, we find that it is intimately related to the jugal and squamosal bones and usually occurs in the region of the junction of these two bones (figs. 3, 4). In *Placochelys placodonta* (fig. 4) it forms a wedge inserted at the upper end of the suture between the jugal and squamosal. The post-orbital also bounds the orbital cavity

posteriorly. In *Dicynodon* the post-frontal occupies a position similar to that of the post-orbital in *Placochelys placodonta*.

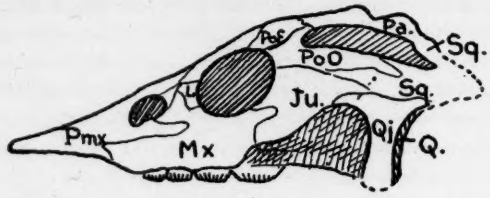


Fig. 4. Skull of *Placochelys placodonta* Jaekel. (After Broom.) *Pmx.* = premaxilla; *Mx.* = maxilla; *Po.f.* = post-frontal; *Po.O.* = post-orbital; *Ju.* = jugal; *Sq.* = squamosal; *Pa.* = parietal; *Qj.* = quadrato-jugal; *Q.* = quadrate.

During the transition from the reptilian to the mammalian form of skull, the post-orbital and post-frontal bones were either lost or suppressed so that they cannot be recognised in the normal mammalian skull. The mammalian zygomatic arch is therefore formed by the zygomatic and temporal bones only (fig. 5).

If one compares the position of the anomalous bone in the baboon skulls with that of the post-orbital bone in a reptile like *Placochelys placodonta*, there is an absolute homology between them as far as position is concerned. In some of my specimens in which the abnormal bone shows a tendency to have grown upwards and forwards towards the orbital cavity (fig. 1, *C*) the resemblance amounts virtually to identity.

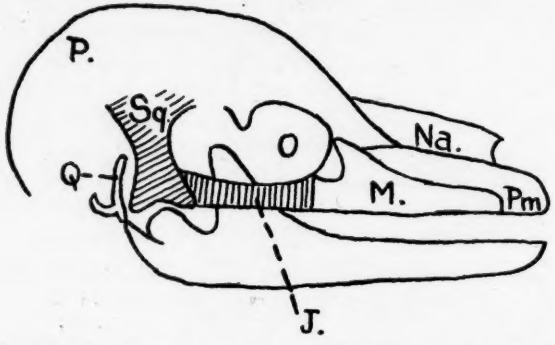


Fig. 5. Diagram to show generalised pattern of mammalian skull. (After Gadow.) *Sq.* = squa mosal; *J.* = jugal; *P.* = parietal; *Na.* = nasal; *M.* = maxilla; *Pm.* = premaxilla; *O.* = orbit.

After considering all these facts I had already come to the conclusion that the anomalous bone in these baboon skulls represents, or is, indeed, simply a recurrence of, the post-orbital bone of the reptilian ancestor of mammals, when I had occasion to study Frassetto's *Lezioni di Anthropologia* and learned therefrom that L. Maggi believes that, in the frontal bone of

the human skull is contained the post-orbital bone of the Crossopterygii, Ganoids, Stegocephalia, fossil reptiles and Gomphodonts. Maggi arrived at this conclusion while studying the ossification of the frontal bone. Each half of this bone is believed by him to ossify from three centres, and each of these to represent a bone of a pro-mammalian creature—the first a supra-orbital, the second a post-frontal and the third a post-orbital. The post-orbital portion of the frontal is, according to this observer, that part lying next to the alisphenoid in front of the pterion, i.e. the zygomatic process and adjacent portion of the frontal bone.

Although I have been unable to see Maggi's original paper on the subject, it seems to me that there is very little evidence for attributing to these centres of ossification a phylogenetic significance. In the first place, after consulting some of the modern standard works on comparative embryology (Graham Kerr, Oskar Hertwig), I have still been unable to ascertain the number of centres from which the cranial bones ossify in reptiles. Before we can attribute to any centre of ossification in the frontal or any other bone a phylogenetic significance, we must be certain that the bone in question ossifies from less centres in the lower animals than it does in mammals. It may be that the frontal bone of reptiles ossifies from several centres, and until the number of separate centres in reptiles is fully known we cannot attribute to any of the three centres of the primate frontal their proper phylogenetic significance. Furthermore, if we attribute to one centre of ossification a phylogenetic significance we ought also logically to attribute to every other such centre a similar significance. This is impossible, for there are more ossification centres in the mammalian skull than there are separate bones in the reptiles with which they may correspond. For example, Albrecht (see Frassetto) found a tripartite zygomatic bone in a human being and he regards the two upper portions of this tripartite bone as representing the post-frontal of reptiles. As already stated, Maggi believes the post-frontal to be incorporated in the frontal. If the latter observer is right, what bones do the parts of Albrecht's tripartite bone represent? There are no further bones in reptiles with which they can be homologous.

If, then, we agree with Maggi or with Albrecht, and the homologue of the reptilian post-orbital and post-frontal bones are already discovered, even if their exact situation—whether in the frontal or zygomatic bone—is unknown, nothing further can be said and the particular osseous element here described can have no explanation.

It would appear more scientific, however, in the present state of our knowledge, to regard the postulates of both Maggi and Albrecht as unproven until the history of the ossification centres in the reptilian membrane bones is more satisfactorily cleared up.

In the case of these baboon skulls, we are dealing with something totally different—with a separate bone in a very precise and topographically important situation from the point of view of homology. It is neither part of

the zygomatic nor of the temporal bone, but is an additional entity. That such a new bone could appear spontaneously in the skull of a primate without some historical background seems impossible. In other words, it is justifiable to attribute to this peculiar osseous element a phylogenetic significance, and the only bone with which it can be homologised is the post-orbital bone of the reptilian ancestor of mammals.

The occurrence of the anomalous bone in such a large number of specimens of *P. porcarius orientalis* is extraordinary. It is to be noted, however, that all the abnormal specimens in the oriental variety came from Mountain Top, Albany, Cape Province, and it is not impossible that they all belonged to the same baboon troop. It would be an attractive hypothesis that one male was originally possessed of the abnormal zygomatic arch and that he transmitted this abnormal structure, through the females, to his male offspring, much in the same way as haemophilia is transmitted on Mendelian lines. The fact that an example of the abnormality was found in the subspecies *occidentalis*, shows that this explanation is not quite complete, but, on the other hand, it serves to strengthen the hypothesis that the anomaly is the homologue of the post-orbital bone.

## SUMMARY

(i) The presence of an anomalous bone in the zygomatic arch has been observed in 20 per cent. of a series of skulls of *Papio porcarius*, all the examples of which except one occurred in the subspecies *P. porcarius orientalis*.

(ii) The bone is not pathological, neither is there any evidence to show that it is a hypertrophic manifestation due to increased functional demands.

(iii) There is evidence which indicates that the new bone is the result of an excess in the processes of normal development.

(iv) This excess in ontogenesis seems to have a phylogenetic significance, viz. the anomalous bone represents the post-orbital bone of the reptilian ancestor of mammals.

(v) The occurrence of this anomaly in the two subspecies of *Papio porcarius* strengthens the hypotheses (*a*) that it is the homologue of the post-orbital bone of reptiles, and (*b*) together with other evidence adduced that some vestigial remnant of the post-orbital is present in the zygomatic arch of all primates and probably of all mammals.

## ACKNOWLEDGEMENTS

I desire to express my gratitude to Prof. R. A. Dart, Head of the Department of Anatomy in this University, for the valuable assistance and kind criticism given to me during the course of this investigation. My thanks are also due to Dr A. S. Strachan for his opinion and to Mr H. Le Helloco for preparing the diagrams.

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# SUPERFOETATION—FURTHER CASES IN PIGS AND SHEEP

By A. D. BUCHANAN SMITH

Since writing the paper entitled "A Case of Superfoetation in the Pig"[1] the following cases have come to the writer's knowledge. As they have considerable bearing upon the subject of superfoetation and superfecundation, it has been thought advisable that they should be placed on record. It is worth noting that the two cases dealing with sheep are the first to have been recorded in this animal. While superfecundation resulting from the services of two rams in one heat period and simultaneous births is not at all rare, there is no previous evidence of superfoetation. In view of this, no pains have been spared to corroborate and test the facts recorded in Case 6, which appears to the writer to be one of considerable importance.

### *Case* 1. *Pig: Aberdeenshire*

Mr Robert Scott, now of Grove House, Bucksburn, Aberdeenshire, when residing at Margaret Cottage, Persley, where he carried on the business of pig breeder, possessed in 1912 a sow which farrowed and reared her litter to six weeks and was still suckling them when she gave birth to a second litter of well-developed pigs. These were, however, tramped to death by the older litter. There were more than four pigs in this litter. The sow had been with the boar for three days and her owner does not recollect her having been with the boar a second time. He states, however, that it was quite possible that the boar could have jumped the wall dividing the two pens.

The above information was furnished by the owner of the sow in response to a letter which had been sent to the editor of the *Aberdeen Press and Journal* requesting information of this case. Previous information regarding this case had been given the writer by Mr Wm. Brown, M.R.C.V.S., of Aberdeen University, who stated that a case of probable superfoetation had been reported to him between 1912 and 1914 in the neighbourhood of the parish of Belhelvie, Aberdeenshire. (Persley is in the adjoining parish of Old Machar.) Mr Brown stated that he was sure that the interval between the births was as much as six weeks and also that the first litter consisted of six and the second of five.

### *Case* 2. *Pig: A Large White Sow*

The following was reported to the writer by Mr John Byers who has charge of the pigs on the farm belonging to Mrs Douglas of Auchlochan, Lesmahagow, Lanark. Towards the end of the year 1923 a Large White

[1] *Journ. Anat.* vol. LXI (1927), pp. 329–332.

sow was mated twice to a Large White boar with an interval of about 21–25 days. Early in 1924 the sow farrowed five young and 24 days later produced another litter of seven, six of which were perfectly normal and healthy but one was much decayed and described as being "black in poke." At this time it was the regular custom in the farm to mate the sows twice in this manner. According to Mr Byers this always produced some runts. On the practice being discontinued, the proportion of such undeveloped types sank to almost nil.

It would seem possible that the decayed "black in poke" pig belonged to the previous litter and was in process of resorbation.

No further reliable information could be obtained.

*Case* 3. *Pig: A Lincoln Sow*

A Lincoln sow belonging to Mr John H. Licquorice, Middle East Farm, Thorney, was mated on 17 December, 1926, to a pure-bred Large White, and may have had access to him subsequently though the owner is inclined to believe that she did not. By him she gave birth 113 days later, on 9 April, to a litter of six. On 2 May, 132 days from the date of her first mating, she gave birth to a seventh pig, who at three weeks old weighed 10½ lb. This is an interesting case and may be equally well explained either by superfoetation or by Kuntz's hypothesis that owing to under-development *in utero*, the pig was not extruded with the remainder of the litter.

*Case* 4. *Sheep: A Cheviot Ewe*

In 1920, on the farm of Ardsier Mains, near Fort George, Inverness-shire, a flock of Cheviot ewes was mated first to an Oxford Down tup and subsequently, though with an uncertain interval, to a Border Leicester tup. In 1921 one of the Cheviot ewes gave birth to a lamb certainly by the Oxford tup. Approximately 6 weeks later the same ewe gave birth to another lamb unmistakably by the Border Leicester tup. Further reliable information of this case could not be obtained.

*Case* 5. *Sheep: A Cross Suffolk Ewe*

A cross Suffolk ewe (Suffolk×Half bred) belonging to Mr J. Stirling, Lempitlaw, Kelso, was put to a Southdown ram on 15 October, 1926 and marked by him on 22 October. While the ram was with her she came in season two or perhaps three times, the last time being just a few days before he was taken away. On or about 10 November, an Oxford Down ram was then put in with her and he served her when she again came in season a fortnight later. According to this last service, between 19 and 30 April, i.e. about five months after this final tupping, she lambed a pair of lambs, the one possessing distinct Southdown characterisations, while the other was like the Oxford. Photographs show an unmistakable difference, especially as regards the colour of the head, the one being light and the other black.

This is a very curious case, but on genetical grounds there is some room for doubt. It is unfortunate that the original ewe was not of a pure breed as then the difference between the two lambs would have been more reliable and the tendency for off-types to be thrown would have been greatly reduced. If, as seems quite likely, the two lambs were by different sires, then it would appear possible to postulate that this was a case of superfecundation, and this conclusion is strengthened by the fact that neither of the lambs appeared to be in any way under-developed at birth. All the other lambs sired by the Southdown sire were, however, born on or before 14 April. Lambs by the Oxford Down ram started coming about 12 April. This presumes that the spermatozoa of the first must have lived for several days in the genital tract of the ewe.

It is, however, equally possible that this is a case of superfoetation.

*Case* 6. *Sheep: A Half Bred Ewe*

On 9 or 10 November, 1926, Mr Raine of Rush Farm, Maunby, Thirsk, Yorkshire, purchased at a local market some ewes which had been intended to be sold fat, but which Mr Raine thought would prove useful to him, as he needed some more breeding ewes to make up his winter flock. These sheep were supposed to be unmated, but the seller gave Mr Raine to understand that it was possible that one or two might have been tupped, either by a Wensleydale ram which had by accident jumped a fence, or else by a Wensleydale ram lamb. At this market Mr Raine arranged to send these sheep which he had just bought to the farm of a neighbour who owned an Oxford Down ram, in order that they might be tupped. This was done and the ewes did not come to Rush Farm till after the middle of December.

One of these sheep, a Half bred, or "North Country" ewe as the Border Leicester Cheviot cross is termed in those parts, gave birth on 7 March to two ewe lambs. She was the first ewe in the flock to lamb, and there could be no doubt but that the lambs were sired by a Wensleydale ram. Three days before she lambed this ewe had been found lying on her back, and the owner at that time formed the opinion that on this account the lambs had come somewhat sooner than he quite expected they would, probably a week or ten days, so he thought. Indeed, he would not have been surprised had they been born dead.

Five weeks and three days later, on 14 April, while still suckling these two lambs, this ewe gave birth to three others. At first the owner thought there must have been a mistake and that the ewe had merely adopted them from another sheep. However, the cleansings of the birth were still hanging from the ewe and no other ewe had lambed within four days previously. The next ewe did not lamb till at least one day later—and very possibly more. These three lambs of the second birth, one ewe and two of sex unconfirmed, were of a different type from the twins of the first birth, and, in the owner's opinion, unquestionably by the Oxford Down tup to which the ewe had been mated after purchase. Mr Raine attempted to wean the two older lambs, but, the

ewe proving inconsolable upon the loss of her first born, these were returned to her, and it was decided to raise the three latter ones by hand. Two of these three died shortly after, on or before 20 April. On or about 1 June one of the elder lambs died of wool ball in the stomach.

On Friday, 10 June, the writer visited the farm and obtained the facts related above. Photographs were taken of the ewe and her two lambs, one of each lambing. Unfortunately, the youngest lamb, the survivor of the three of the second birth, died at about this moment, probably owing to over-nourishment from the milk bottle. There was sufficient evidence to show a big difference between the two lambs. Whereas the one of the first birth by the Wensleydale possessed a white face, that of the second by the Oxford was speckled with brown marks, as is customary in such a cross. While the fleece of the elder was open, long and in locks, that of the younger was very much shorter, denser and more closely crimped. The fleece of the elder extended well down the legs to below the knees and hock, while the legs of the younger were practically clean of wool. In these as well as in other details, such as the shape of head, colour of legs, etc., the difference was remarkable.

On this day also the last ewe in the flock was lambing, and the writer took the opportunity of rounding up the flock and checking every ewe and her lamb. Every ewe had one or more lambs. Two ewes had lost their own lambs, and had been given lambs of other ewes, their own having been buried. Mr Raine assured the writer that no ewes had died. All these facts can be vouched for by several of Mr Raine's neighbours who were informed of this occurrence and expressed their surprise and scepticism, but on further investigation also found the facts to be essentially as stated above.

The period of gestation in sheep, according to Lydekker (1912) varies in European breeds from 144 days in Southdowns to 150 days in the case of Merinos, while Youatt (1859) gives it as roughly five months, or 152 days, and this latter opinion is more in consonance with the experience of the majority of sheep raisers in this country. According to Marshall (1922, p. 42) the oestrous cycle in the sheep is of considerable variability and extends from 13 to 18 days, though in mountain breeds such as the Blackface it extends to 21 days: he quotes E. Neubergen as saying that it may be as much as 30 days. In practice it is reckoned as three weeks, or from 18 to 21 days.

The salient points of this case may be summarised as follows:

Up to 9 or 10 November, 1926, it was possible for the ewe in question to have been tupped by a Wensleydale ram. There was no opportunity for her to have been tupped by a ram of any other breed.

After that date she was put on another farm in company with an Oxford Down ram. There was no other ram on this farm.

She was the first ewe to lamb, which she did on 7 March, so that there can be no question of other lambs having been adopted by her owing to her having given milk while still pregnant. Allowing ten days for the probability of her having lambed early owing to having lain on her back, this would give the

first mating and conception date as somewhere around 17 October. These lambs were typical of the Wensleydale Half bred cross.

On 14 April, she lambed again. No other ewe in the flock lambed around her time. The afterbirth was observed while still attached to her. The lambs at this birth were quite unlike those of the previous birth and showed clear traces of an Oxford Down sire. The date of mating and conception which led to this birth was probably around 14 November.

## DISCUSSION

The period between the first and second lambings was 38 days, or if the first lambing be considered to have been premature by ten days, then it would be 28 days. The dioestrous cycle of the sheep is around 18 days, and rarely, though occasionally, as much as 30 days.

From this evidence the writer is unable to see how this case could possibly be explained by arrested development without foetal atrophy. The genetical evidence disposes of the possibility of the ovum lying dormant during the early months of gestation as indicated by Marshall (p. 43, footnote) in roe-deer. And further, since the period between the two conceptions amounted to at least 28 days, and may have been as much as 40, it is practically impossible to account for it by superfecundation. Indeed, it is only possible to explain this as a case of superfoetation, and as such is considerably stronger than the case in the pig already described by the present writer. It is worth noting that it appears likely that the ewe came in season and ovulated at a distance in time of two dioestrous cycles: and this appears also to have occurred in the Cheviot ewe in Case 4. Whether the fertilised ova of each birth were contained in separate horns of the uterus must remain a matter of speculation.

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# THE DURAL RELATIONS OF THE GASSERIAN GANGLION WITH REFERENCE TO A NEW METHOD OF SURGICAL APPROACH

By ROBERT D. LOCKHART, Ch.M.
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This region is not well described by text books of anatomy or surgery.

The dura mater of the posterior aspect of the petrous bone near the apex is prolonged forwards like a glove investing the roots, ganglion, and divisions of the fifth nerve, to lie upon the upper surface of the apex of the petrous bone and of the sphenoid's great wing near the pituitary "door step," and to extend upwards fully half the height of the cavernous sinus, thus forming a good portion of the lower and lateral wall of the sinus, the whole extent of the glove or cave of Meckel being concealed by the dura of the mid-cranial fossa, fig. 1. While the lateral wall of the cave is very adherent to the over-

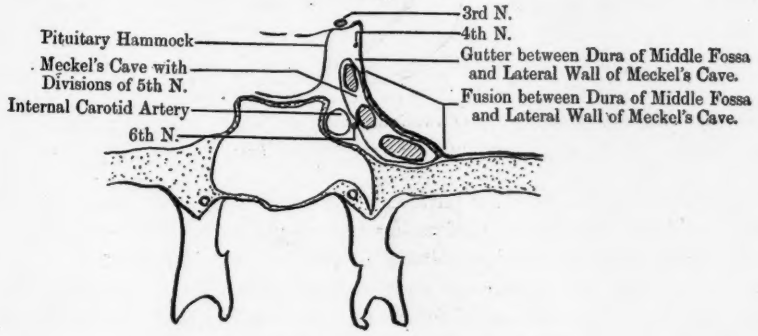
3rd N.
4th N.
Pituitary Hammock
Gutter between Dura of Middle Fossa and Lateral Wall of Meckel's Cave.
Meckel's Cave with Divisions of 5th N.
Fusion between Dura of Middle Fossa and Lateral Wall of Meckel's Cave.
Internal Carotid Artery
6th N.

Fig. 1. Coronal section through pituitary fossa.

lying dura of the mid-cranial fossa, the latter membrane can be carefully dissected apart as a flap to display the cave in position. Proof of the possibility of cleavage lies in the facts that the cave is an evagination of the dura of the posterior cranial fossa under that of the middle fossa; that the blood in the cavernous sinus laps over the upper border of the cave into a little gutter as shown in fig. 1, and when this border reaches high enough to fuse with the diaphragma sellae, as may happen, fig. 2, the sphenoparietal sinus runs back between the dura of the middle fossa and the lateral wall of the cave opening into the posterior part of the cavernous sinus together with the superior petrosal sinus; and lastly, that the superior petrosal sinus insinuates

itself between the wrist of the glove, that is the neck of the cave, and the dura of the middle fossa to splay, at this point, like an estuary into the back of the cavernous sinus. Narrow at the entrance transmitting the roots of the fifth nerve, the cave widens to hold the ganglion and its branches; a probe inserted between the lateral side of the ganglion and the cave reaches forwards to the same plane as that of the anterior wall of the pituitary fossa, laterally wards to the foramen ovale, and upwards, fully half the height of the cavernous sinus, without much resistance. While the lateral side of Meckel's pocket is easily freed from the ganglion and its divisions, the medial wall is adherent, particularly to the first division and the anterior part of the ganglion.

At present, surgeons approach the ganglion by burrowing under the dura mater of the mid-cranial fossa, until the nerve structures are reached, identifying the foramen spinosum and the foramen ovale as guide posts in the process. Oozing may be encountered; haemorrhage from the middle meningeal artery is difficult to control by plugging the foramen spinosum, and in some cases there appears to be a haze of uncertainty as to whether the ganglion

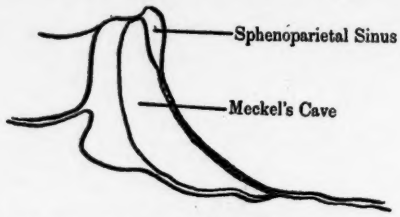


Fig. 2. Coronal section showing a variation, in Meckel's cave, rising high enough to fuse with the Diaphragma Sellae.

has been got or not, until the patient is examined next day. Surgeons state that the main difficulty in performing this operation is to be quite sure of dividing all the nerve because of its adherence to the dura mater.

The new method suggested is an intradural approach, immediately above the dura lining the mid-cranial fossa. Bearing in mind that the lateral wall of Meckel's cave is fused to the lateral wall of the cavernous sinus, an antero-posterior incision is made through the two fused layers to expose the roots, ganglion, and divisions. It is not even necessary to expose these structures, because a suitable instrument inserted into the posterior end of the slit in the dura can hook the roots into the incision as cleanly as a pea from a pod. In no dissecting room case has the dura been seen adherent to the roots of the nerve. If the incision is carried too far back the superior petrosal sinus may be tapped, though this may even be divided between clips to secure a better view of the roots.

The obvious advantage of this intradural approach is the avoidance of any trouble with the middle meningeal artery and the saving of time spent tunnelling under the dura mater. The disadvantages suggested are difficulty

of orientation when the signposts are concealed, and difficulty of retracting the brain sufficiently without damage. The orientation difficulty may be met by prodding the floor of the mid-cranial fossa latero-medially until a slight yielding indicates the transition from dura upon bone to dura upon cave, or still more simply by pricking step by step with a needle latero-medially until the lowest part of the cave is punctured; the one necessary point is to keep the incision low down on the wall of the sinus on the level of the floor of the middle fossa. With regard to sufficient retraction of the brain, as this operation is conducted at the same level as the one at present in vogue, any resulting damage can hardly be appreciably greater by this method.

One anatomical point cited by C. H. Frazier in Keene's *Surgery*, v, 964, that the foramen spinosum frequently lies on a plane anterior to the foramen ovale, has not been observed in the examination of 350 skulls.

Fig. 1 purposely shows the third nerve resting on the dura mater canopy of the four-poster pituitary bed. It enters the sinus by dipping under the anterior clinoid process. Most text-books show cross-sections of the pituitary fossa with the third nerve in the cavernous sinus, but very frequently the nerve pursues the course illustrated.

# CONGENITAL ABSENCE OF THE GALL BLADDER

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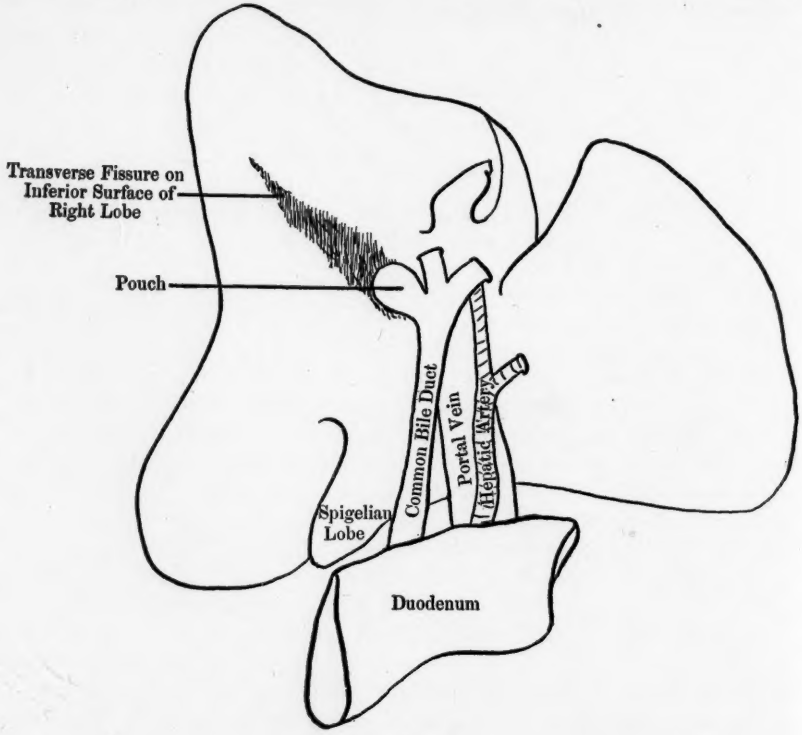
Pathologists (1) state that absence of the gall bladder is very rare in man, and although quite a number of cases are recorded (2) the abnormality is uncommon enough to warrant the description of the present case.

The liver showing this variation was removed from a woman of 24 years who died of lung abscess.

The common bile duct shows a little pouch suggestive of an arrested attempt to produce the gall bladder in the normal position. A deep furrow runs from the porta hepatis to the right on the inferior surface of the right




Inferior surface of liver.

lobe suggestive of a similar fissure seen in the lower monkeys, a little peak projects from the under surface near the anterior border, and there is a rather large downwardly projecting Spigelian lobe. Apart from these features the liver is normal, and the dissection of the hepatic ducts into the liver substance displays no further sacculations. Some regard the general appearance of this liver as foetal in type. The subject showed no abnormality except absence of the gall bladder, although this defect has been seen associated with such groups of variations as atresia of the duodenum and of the left ureter, cystic kidneys, and anomalies of the ear and palate (3); atresia ani and absence of the right thumb (4); supernumerary spleen (5); imperforate anus with megalocolon (6). Such anomalies as double gall bladder with single neck and two cystic ducts, and gall bladder on the antero-superior surface of the liver are recorded (7, 8).

The unsatisfactory explanation that the absence is due to early obliteration has been advanced. Partial obliteration of the gall bladder and of the cystic duct associated with hare lip, cleft palate, and anomalies of ears, hands and heart has been seen in the foetus (9) as well as many (10) foetal cases of obliteration of the bile ducts, probably luetic (2).

The condition has been considered atavistic in man, as the gall bladder is normally absent in some animals.

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# A NOTE ON THE TELEOSTEAN ADRENAL BODIES

By SWALE VINCENT and F. R. CURTIS

*(From the Physiological Laboratory, Middlesex Hospital Medical School)*

The bodies now known as the corpuscles of Stannius in Teleosts were first described by the author whose name they bear, in 1839, and definitely designated by him "Nebennieren" (1). The view that this designation was correct seems to have been accepted by the few investigators who devoted any attention to the subject. Thus Ecker (2) in 1846 refers to the bodies as the corpuscles of Stannius, and gives an excellent drawing of their structure. On the other hand some zoologists and comparative anatomists seem to have overlooked the work of Stannius, Ecker, and others, and put forward quite erroneous statements about the bodies in question. Thus Weldon (3) thought that the adrenals were frequently absent in Teleosts, and that the lymphoid "head-kidney" took their place. Beard (4) was also under the impression that nothing corresponding to the adrenal bodies could be discovered in Teleosts or Ganoids. These views were refuted by one of us in 1896 (Vincent (5, 6)), and it was shown that the corpuscles of Stannius which presented the best claims at that period to be called adrenal bodies, are universally present in Teleosts, quite independently of the degree of development of the lymphoid "head-kidney." The corpuscles of Stannius are pale, spherical bodies near the caudal end of the kidney, on its ventral or dorsal surface, and appeared to have roughly the same structure as the interrenal of Elasmobranchs, and the cortex of the adrenal of higher Vertebrates.

In 1908, E. Giacomini (7) put forward another claimant for the position of teleostean adrenal cortex, namely, groups of glandular-looking cells in the lymphoid "head-kidney," and stretched out along the blood vessels in this region. Since that time it has been customary to refer to the anterior and posterior cortical adrenals in these Fishes.

The work of Giacomini seemed to minimise the importance of extirpation experiments carried out upon the corpuscles of Stannius, in which eels were found to live indefinitely after extirpation of these bodies (Vincent (8)).

Giacomini (9), however, called attention to important differences in structure between the two kinds of body, and this is admirably shown in his illustrations. He also states that the development of the two structures is quite different. He inclines to the view that the "anterior interrenal" is more likely to be the representative of the adrenal cortical tissue in Teleosts.

More recently Ramalho (10) has studied this problem, and from cytological considerations has come to the conclusion that it is Giacomini's anterior

interrenal body which ought to be considered as the true adrenal in Teleosts, and the homologue of the adrenal cortex in Mammals. His general conclusion is as follows:

"Les corps de Stannius, généralement considérés comme des organes interrénaux, sont si différents du vrai tissue interrénal que, comme Giacomini, il se refuse à accepter les vues classiques."

In view of the fact that a memoir by one of us (Vincent (6)), written in 1895, was the first account of the adrenals in Fishes published in this country, it occurred to us that it would be interesting to see if these newer views could be confirmed.

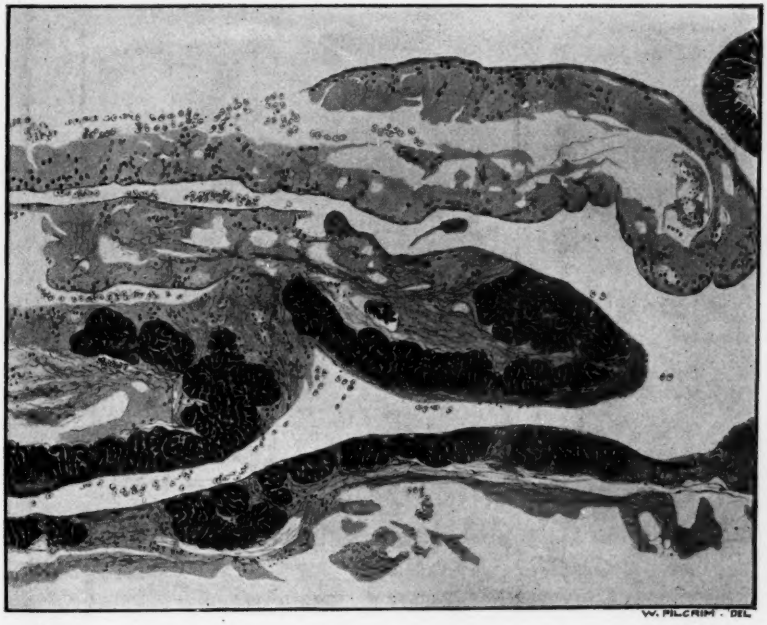


Fig. 1. Anterior interrenal of *Anguilla anguilla*. Low-power. ×90.

The present communication records our investigation of the microscopic structure of the corpuscles of Stannius and of the "anterior interrenal" bodies of Giacomini.

We have confined our attention to a study of the structure of these bodies in the common fresh-water eel (*Anguilla anguilla*) because this fish is conveniently obtained in a living state.

The anterior cortical adrenal is found in the form of elongated columns of cells, usually two or three deep, but occasionally forming larger masses.

These are stretched out along the blood vessels or occupy an irregular position in the substance of the "head-kidney" (see fig. 1).

Under a moderately high power the cells appear uniformly stained or very finely granular (figs. 1 and 3).

Measurement of this tissue shows that the cells are on an average about 15 $\mu$ in length, and 8 $\mu$ in width. Where the cells are arranged in the form of

Fig. 2. Stannius corpuscle of *Anguilla anguilla*. Low-power. ×90.

alveoli, which is not infrequently, the alveolus is usually about 100 $\mu$ in one direction, and 49 $\mu$ at right angles to this.

The Stannius corpuscles are paired bodies placed on the ventral or dorsal surface of the kidney. A low-power view of this tissue shows a collection of

Fig. 3. Anterior interrenal. High-power.

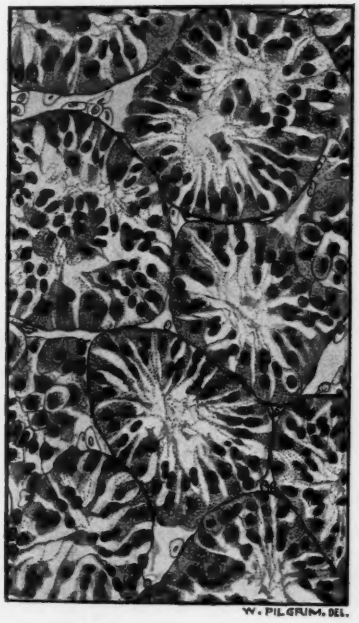


Fig. 4. Stannius corpuscle. High-power.

(*a*) (*b*)

Fig. 5. (*a*) Anterior interrenal. ×1600. Drawing of Golgi apparatus. (*b*) Stannius corpuscle. ×1600. Drawing of Golgi apparatus.

alveoli with very characteristic spaces in the middle (see fig. 2). These spaces were drawn and described by Vincent (*loc. cit.*) and are also recorded by Giacomini and Ramalho but their meaning remains to be determined.

The alveoli are approximately 100 $\mu$ by 70 $\mu$ in diameter. The cells measure about 22 $\mu$ in length, and 11 $\mu$ in width.

Under the higher powers of the microscope the cells of the Stannius corpuscle are seen to be granular, but more finely so than those of the anterior interrenal. It is possible that the spaces above mentioned in the alveoli of the Stannius body may be due to shrinking during preparation. If so, this fact is a striking histological difference from the anterior interrenal which during the same preparation shows no such shrinkage (see fig. 4).

Preparations of these two tissues by the methods which show Golgi apparatus have been obtained by the generous co-operation of the late Dr C. da Fano of King's College, London. As the drawings show, the network is markedly different in the two cases. In the Stannius cell, the network is arranged as a prominent closely fitting cap on the nucleus, usually on the opposite side to the nucleolus. On the other hand, the Golgi structure in the anterior interrenal cell is rather small and insignificant. It is quite compactly arranged, and is not so closely related to the nucleus as in the Stannius cell (figs. 5 *a* and *b*).

An inspection of our illustrations will, we imagine, lead to the conclusion that the "anterior interrenal" and the "corpuscle of Stannius" are not separated portions of the same organ or tissue, but represent structures differing essentially in their nature one from the other.

It thus appears that the corpuscles of Stannius, for so long regarded as the homologues of the adrenal cortex in Teleostean Fishes, have almost certainly no relationship whatever to this organ. The true homologue of the adrenal cortex in this order of Fishes is the "anterior interrenal" of Giacomini. Its proper title would appear to be "the cortical adrenal body." This conclusion leads us into a serious dilemma in the matter of the corpuscles of Stannius. The morphological position of these bodies is problematic, and their physiological significance cannot for the time being be even surmised. In the experiments of Vincent cited above, it was found that these bodies are not essential to the life of the animal.

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# THE HISTOLOGY OF THE GIRAFFE'S CAROTID, FUNCTIONALLY CONSIDERED

By K. J. FRANKLIN, D.M., and F. HAYNES, M.A.

(*From the Pharmacological and Physiological Laboratories, Oxford*)

THROUGH the courtesy of Dr Chalmers Mitchell and Dr Vevers, and the facilities kindly afforded by Dr Scott and Dr Beattie, one of us had recently the opportunity of examining the carotid artery of a young giraffe at the Zoological Gardens.

The object in view was to find out what structural mechanism existed for overcoming hydrostatic pressure in blood vessels, and the neck vessels of the giraffe seemed most likely to give the answer. The intermittent output of the heart, however, must also be taken into account in evaluating the results.

The macroscopic appearances of the upper and lower parts of the artery suggested the presence of a larger amount of elastic tissue in the lower, appearances analogous to those in the carotid of the ostrich (Dr Beattie). The comparative histology of the two portions, given in detail below and illustrated by microphotographs, amply corroborates these suggestions.

## I. THE HISTOLOGY OF THE UPPER PORTION

In the intima, the elastic fibres supporting the endothelium and its thin collagen layer interlace. The alternate layers of delicate collagen and elastin beneath this indicate the commencement of the media. The media proper is divided into two parts, an inner composed of muscle bundles with much elastin, and an outer consisting of larger bundles of muscle separated from each other by septa of stout collagen fibres containing both fine and coarse elastic fibres. The muscle fibres have a circular direction.

The adventitia is sharply demarcated from the media, containing no muscle fibres, and being composed solely of a feltwork of very robust collagen fibres enclosing an equally complex meshwork of elastin. The outer portion of the adventitia is almost entirely free, however, from elastic fibres.

Fair numbers of vasa vasorum run in the adventitia, especially in the outer half of it.

In transverse section, the two sides of the vessel differ slightly, the elastic fibres being less highly developed in the inner portion of the media in one half than in the other.

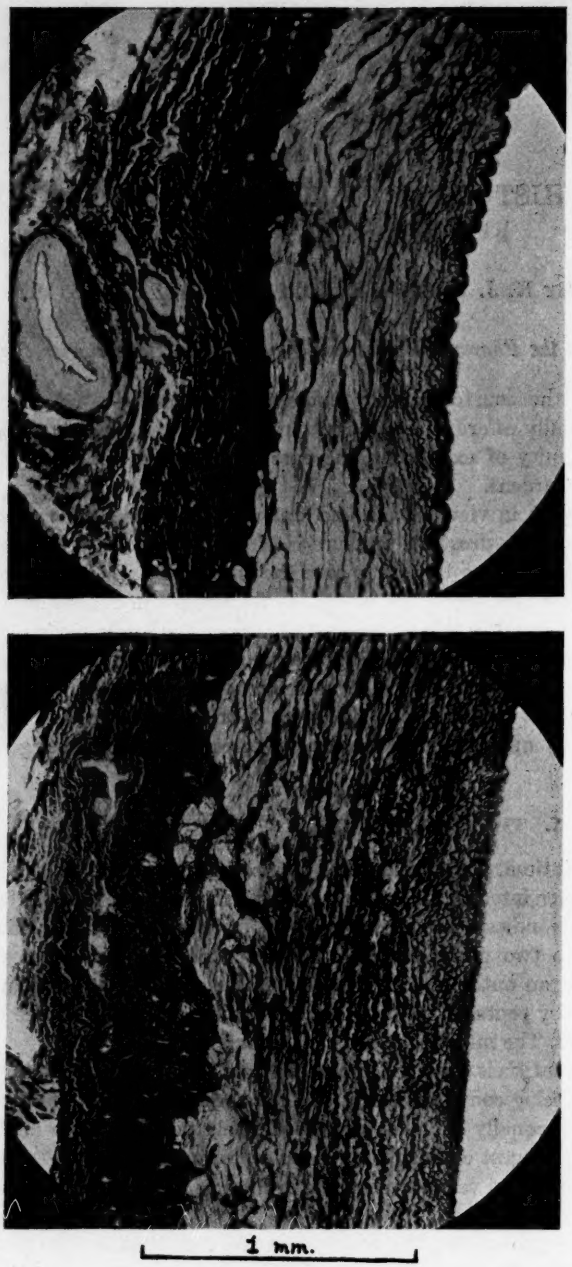



Fig. 1. Untouched microphotographs of the two portions of the giraffe's carotid, magnified 42 diameters. Paraffin sections of 8 $\mu$, stained Weigert's phenol-fuchsin and Schmorl's modification of van Gieson's stain. The photograph of the upper portion is placed above that of the lower, more elastic, one.

## II. THE HISTOLOGY OF THE LOWER PORTION

The endothelium rests on a fine collagen meshwork, supported by very robust elastic fibres. Beneath this stratum are layers of stout elastin alternating with delicate collagen and a gradually increasing, but always slight, amount of smooth muscle. The intima is not in any way demarcated from the media. The media is roughly divisible into three parts, which offer a gradual transition from one to another. The parts are of about equal thickness; in (*a*), the innermost, predominantly coarse elastic fibres alternate with fine collagen fibres and a little circular muscle; in (*b*), the middle layer, the proportion of muscle and collagen (which is here in coarser fibres) is increased, and fine elastic fibrils cross the muscle bundles, uniting adjacent elastic septa; in (*c*), the outer zone of the media, there is much circular muscle and very little elastin. The collagen, in stout fibres, divides the muscle into fairly large bundles.

The adventitia is in every way similar to that of the upper portion of the vessel.

## III. COMPARISON OF THE UPPER AND LOWER PORTIONS

The outstanding differences between the elastic (lower) and muscular (higher) parts of the carotid artery of the giraffe are confined to the media. This, in the lower part of the vessel, may be regarded as predominantly elastic, while in the upper part the elastin is subsidiary to the muscle.

## SUMMARY

The structural mechanism in the giraffe's carotid by means of which the mechanical conditions in this vessel are counteracted consists of a very great increase in the elastic tissue in the lower portion. In the words of John Hunter, "such parts as have yielded to the action of some other power, as gravitation, are brought back into what may be called a natural state, and are retained there by elasticity, till that power is again overcome by another, as in the necks of some animals (1)."

## REFERENCE

(1) Palmer's edition of the *Works of John Hunter*, 1837, vol. III, p. 153.

# TWO CASES OF CONGENITAL DEFORMITY OF THE UPPER LIMB

By L. R. SHORE

## I. A FEMALE CHILD, AGED 7½, WITH A DEFORMITY OF THE LEFT HAND

The hand is grossly deformed, as it seems, by the lack of the middle three fingers, including the metacarpal bones; the thumb and little fingers are reduced, but recognisable; bony elements can be felt in their proximal parts. The thumb has a small nail near its end, though no skeleton can be felt in its terminal segment. Some gripping power is obtained by approximation of thumb and little finger elements across the palmar surface of the hand.

The skiagram shows a much reduced metacarpus; the carpus is normal. The metacarpal of the thumb has a well-marked basal epiphysis, but a much reduced shaft; the intermediate phalanx is a mere rudiment. The metacarpal of the little finger is much reduced, but apparently has a small scale-like epiphysis for the head.

It is remarked that the ossific process in the basal epiphysis of the thumb is larger on the side of the abnormality.

The deformity noted is the only skeletal abnormality in a healthy child. Three other children in the family and the parents are all normal.

## II. A MALE CHILD, AGED 7½, WITH A CONGENITAL DEFORMITY OF THE LEFT ARM

The left forearm is reduced to a stump about an inch in length; the end is rounded but puckered, and has a small wart-like projection in the centre. The stump is freely movable, and to palpation the joint seems normal. Rudiments of radius and ulna can be felt.

Skiagrams show the following:

(1) In the elbow of the deformed limb the normal skeletal elements are present, except the epiphysis for the internal condyle of the humerus, which is lacking.

(2) Reduction of humerus and diminutive size of the radius and ulna. While the condyles of the humerus are hardly appreciable, the lateral view shows that the olecranon and coronoid fossae are normally developed.

(3) The ossification of the capitellum is equal on the two sides.

(4) The ossific centre for the head of the radius is present on the side of the abnormality, and seems larger than the other.

As in the other child, that described is the only abnormality. Four other children and the two parents are entirely normal.

## DISCUSSION

It is assumed that such deformities as those described result in reduction of the normal influences of pressure and traction; the obvious deficiences of the affected member and the compensatory use of the normal limb lend support to this assumption.

Two conditions of epiphyseal ossification are found, and are contrasted.

(1) In Case II there is suppression of the normal centre for the internal condyle of the humerus.

(2) In Case II the ossification for the head of the radius, and, in Case I, that for the base of the first metacarpal, are in excess of the normal.

The large size of the ossific centres for the head of the radius, and the base of the first metacarpal suggest that normal strains are requisite to reduce epiphyseal ossification to normal proportions.

I have been unable to obtain any further cases of congenital deficiency of this type for comparison.

## INTRA-UTERINE AMPUTATION

The Museum of the Royal College of Surgeons contains five specimens, which occurred in three individuals, and are in some respects comparable to the cases described.

No. 460, of a 5th month female foetus with deficiency below the knee. There was also defective development of the face and a fusion of digits of the left hand.

No. 462. A foetus with a deficiency just below the right elbow. The integument of a terminal dimple seems to be adherent to underlying muscle.

No. 463. The left arm of the same foetus deficient below the middle third of the upper arm.

No. 464. The left leg of the same foetus, deficient just below the condyles of the femur. A wart-like tubercle is present near the end on the posterior and medial aspect of the limb-stump.

No. 464 I. The bones forming the stump of the right leg of a boy aged 11 years. The leg is deficient 6 inches below the knee, and there is fusion of the tibia and fibula. Other associated defects were:

Right hand—three fingers and thumb lacking.
Left hand—4th and 5th digits lacking.
Left leg—toes defective.

The catalogue of the Museum of the Royal College of Surgeons contains the following words: "'Hemimelia.' The preparations classed under this term are usually regarded as intra-uterine amputation; there is perhaps no reason for so regarding them except their superficial similarity to the stumps of amputated limbs."

It is difficult to offer an opinion, if cases such as the two I describe, and the specimens in the Museum of the Royal College of Surgeons actually arose

by a process of amputation *in utero*. That amputation of a limb may take place *in utero* is placed beyond doubt by a recent report in the Medical Press. In the *British Medical Journal* of May 22nd, 1926, Dr W. Hornsby of Greenock describes the 8th parturition of a multipara:

...in manipulating for a foot my finger came against a very sharp end of bone, and I also felt a small foot and leg lying free inside the uterus. I secured the normal foot and easily delivered a live boy, my only fear being that the uterus might get damaged by the pointed stump of the femur. I then removed the detached foot and leg.

On examining the child I found that the left leg was amputated about the middle of the thigh, the stump being completely healed except that the femur projected about a quarter of an inch—a condition similar to that found during the war after circular amputations had been allowed to granulate. The amputated part was macerated and much smaller than the other limb—about five months as compared to seven months and a half.

There was nothing abnormal about the placenta, which came away easily within ten minutes of the birth. The cord was somewhat longer than usual, and very thin....

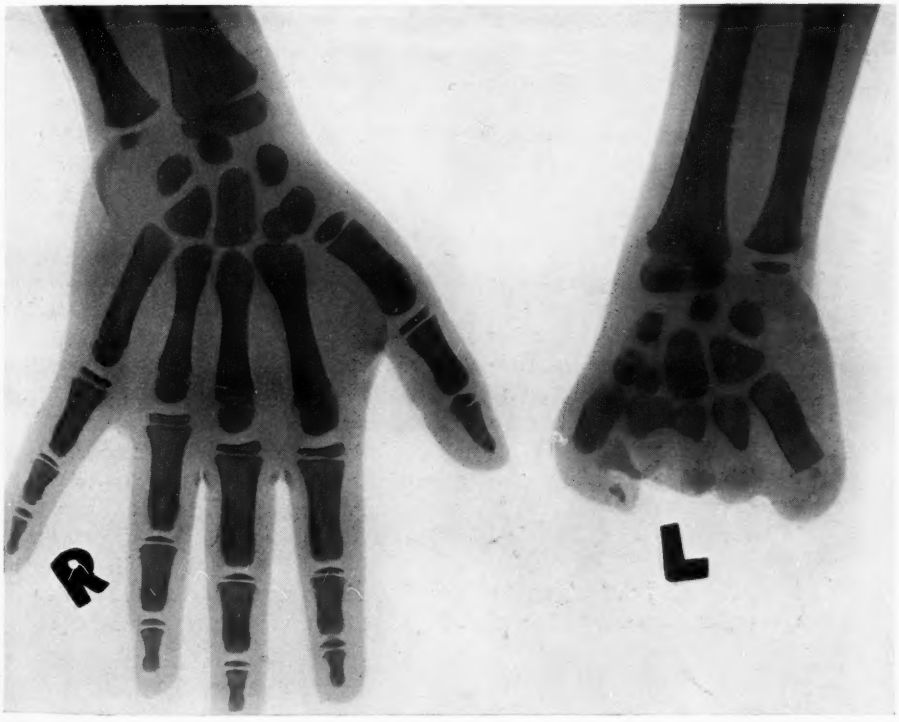
Up to the seventh child there was no trouble with any of her babies.... All the children were born alive, but small....She is rickety and has a justo-minor pelvis.

Among the points of interest in this somewhat rare case are that the child was born alive, it cried feebly for ten minutes, showing that the constricting force was not likely to have been the umbilical cord, as otherwise a dead child would have been expected; if the force was sufficient to cause amputation it would have been sufficient to stop the flow of blood in the vessels of the cord. It is conceivable, however, that by slow pressure, the tissues being soft, especially the bone, amputation might take place without the death of the child, and the condition of the cord might support this view. The stump being healed is sure proof that amputation took place some month or two previously, and this conclusion is strengthened by the size of the amputated part.

As regards Case II, here described, and No. 462 in the Museum of the Royal College of Surgeons, it is suggested that the terminal tubercle on the shortened member may be of some significance. A terminal tubercle seems a more likely result from healing of an amputated stump by granulation than from congenital deficiency. Dimpling is presumably due to cicatrix as in specimen 462. This is seen in my Case II and Nos. 462 and 464 in the Museum, but was absent in Case I and in the other specimens.

In Dr Hornsby's case the femur projected through the end of the stump. The probable end of such a case, if the child had lived is a matter of conjecture; but on the analogy of wounds, it is easy to imagine a central cicatrix or tubercle.

If these cases are to be classified as "true amputation *in utero*" on the one hand, and "false amputation, or hemimelia" on the other, it is suggested that the terminal tubercle or cicatrix may be a point of difference.




SHORE—Two Cases of Congenital Deformity of the Upper Limb

UNIV. OF MICH.

# ANATOMICAL RECORDS

## SOME ANOMALIES OF ORIGIN OF THE VERTEBRAL ARTERY

By A. ANANTHANARAYANA IYER, B.A., M.B., B.S.
(*Senior Demonstrator in Anatomy, Medical College, Madras*)

During the years 1912 to 1926 the following anomalies in the origin of the vertebral artery have been recorded in the "Abnormalities Book" in the Anatomy Department of the Medical College, Madras (India). In this period 828 bodies were dissected.

| No. | Date | Description of abnormality |
|---|---|---|
| I | 20. xi. 1912 | The vertebral artery of the right side springs from the right common carotid at level of the intervertebral disc between 7th cervical and 1st dorsal vertebra |
| II | 7. xii. 1917 | The left vertebral arises directly from the arch of the aorta |
| III | 9. xi. 1918 | The left vertebral arises directly from the root of the subclavian very near the aortic arch |
| IV | 15. xii. 1918 | The left vertebral arises directly from the arch of the aorta |
| V | 27. i. 1919 | Two left vertebral arteries, one arising from the arch of the aorta, the other from the left subclavian artery in the normal position. The one in the normal position is a small vessel |
| VI | 3. iii. 1919 | The left vertebral and the left internal mammary arise directly from the arch of the aorta instead of from the subclavian |
| VII | 26. viii. 1926 | The left vertebral took origin from the aorta between the origins of the left common carotid and the left subclavian. It enters the foramen of the transverse process of 5th cervical vertebra |
| VIII | 29. viii. 1926 | The left vertebral takes origin from the aorta at the upper angle of the junction of the left subclavian with the arch of the aorta. It enters the foramen of the transverse process of 5th cervical vertebra |

It is recognised that the cervical portion of the vertebral artery is formed by a series of longitudinal anastomoses between the upper seven dorsal segmental arteries and the disappearance of the proximal portions of the upper six segmental arteries. The seventh pair of segmental arteries takes part in the formation of the subclavian artery, the left forming the whole of the left subclavian and the right a considerable portion of the right one.

The explanation offered of the above anomalies is as follows:

In the cases II, IV and VII reported above, the left vertebral takes origin directly from the aortic arch. Robinson, in Cunningham's *Text-Book of Anatomy*, explains this anomaly by supposing that the proximal part of the primitive subclavian has been absorbed into the aorta and as a consequence the vertebral and the subclavian have come by separate origins from the aorta. Cairney, while admitting that such a process is by no means impossible, raises the objection that there is no reason why such an absorption should occur in a few cases and not in all. He suggests that the vertebral from its inception might have incorporated the stem of the 6th segmental artery, while the subclavian has incorporated the stem of the 7th segmental in the usual manner. Rather than consider these two explanations as antagonistic, each might be considered as being true in its own way.

Cairney's objection to the absorption of the primitive subclavian on the ground that there appears to be "no reason why it should occur in some cases and not in all," merely shows the limitation of our knowledge. A case like III reported above, where the left vertebral springs from the root of the subclavian very near the arch

of the aorta, and also case VIII, where the left vertebral arises from the aortic arch at the junction of the subclavian with the arch of the aorta, show a stage in a process of absorption, one on which the ultimate result would be to leave a left vertebral taking a separate origin from the aortic arch. In case VI where the left vertebral and the left internal mammary arise directly from the arch of the aorta we seem to see a process of absorption of the primitive subclavian going a little further so as to include the internal mammary artery.

But we find a different state of affairs in case V. There are two vertebral arteries, one arising from the arch of the aorta, the other from the left subclavian. Unfortunately the record gives no information as to the further course of the two arteries. But it is clear so far as it goes. The small vessel from the subclavian represents the normal vertebral. The additional left vertebral which took origin from the arch of the aorta could not be obtained by a process of absorption of the primitive subclavian. It must represent a persistent 6th dorsal segmental artery which disappears in normal cases. Cairney cites the case of Gladstone and Wakeley, in which the left vertebral, in a human embryo, 17 mm. long, had an independent origin from the left dorsal aorta about midway between the left common carotid and the left subclavian arteries. Case V recorded above is another piece of evidence in support of Cairney's explanation.

Only one other case remains to be discussed: case I in which the right vertebral artery took origin from the right common carotid. If we suppose that the 6th segmental artery persisted and also the 5th aortic arch on the right side, then an explanation becomes easy. The 4th right aortic arch, part of the right dorsal aorta and the right 6th segmental artery would form the right vertebral and it would then take its origin from the common carotid. The right 5th aortic arch, part of the right dorsal aorta and the right 7th segmental artery would give rise to an apparently normal right subclavian.

Finally, I wish to thank Dr T. Sundara Reddy, F.R.C.S. (I.), Professor of Anatomy, Medical College, Madras, for his kind permission to publish these notes.

SUMMARY.

Eight cases of abnormal vertebral artery, seven on the left side and one on the right, are recorded.

An explanation of the abnormalities on the basis of the development of the artery is attempted.

A left vertebral that springs from the aortic arch between the left common carotid and left subclavian may be either a result of the absorption of the primitive subclavian or due to a persistence of the 6th left dorsal segmental artery.

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# REVIEWS

*Topographische Anatomie.* O. SCHULTZE. Third edition prepared by Dr WM LUBOSCH. Published by Lehmann, Munich.

The subtitle decribes this book as an atlas and short textbook of topographical and applied anatomy. In preparing this new edition, which is practically a new book, Dr Lubosch set himself the task of incorporating in a single volume enough scientific matter to give the medical student some idea of how the form of the body is derived; enough topographical anatomy to familiarise him with the detailed structure of the body; and finally enough applied anatomy to show the immediate bearing of the facts of anatomy on the problems of medicine and surgery.

This comprehensive programme has indeed been most successfully accomplished within the 300 odd pages of the book. The text is illustrated by 405 pictures. These include many excellent X-ray photographs and an abundance of coloured illustrations. Indeed, like so many other excellent German textbooks, such as Braus, Spalteholtz, etc., the book excels in the abundance, clarity, and beauty of the illustrations.

The antimerism and metamerism of the body with its derivations and modifications in different areas of the body are separately treated, but it is quite a feature of the book that in the discussion of regional anatomy everywhere our knowledge of the factors which have played a part in producing the form of the region in question receives consideration. The clinical items introduced are such as are immediately dependent on the preceding anatomical text. Altogether we think this book deserves very high praise for the success which has attended its preparation in that it exhibits how much real anatomy can be accommodated in a book of brief dimensions.

*Anatomie Topographique du Système Nerveux Central.* G. GUILLAIN et I. BERTRAND. Masson et Cie. Paris, 1926. Pp. 322. 60 plates. Price 95 francs.

This volume, demonstrating the form and structure of the central nervous system, has been compiled primarily to assist neurologists and pathologists in the localisation and interpretation of morbid processes. It will also prove of interest and value to anatomists, since it contains an admirable series of sixty original illustrations, displaying the external features and structures of sections at all important levels through the brain and spinal cord. These illustrations will be of the greatest use to students who are studying sections of the central nervous system after they have completed a preliminary gross dissection of the brain, and the book may be confidently and warmly recommended for

this purpose. Most of the illustrations are intended to demonstrate only naked eye appearances, but a few are included which represent the histological structure of such regions as the cerebral and cerebellar cortex. All the plates are perfectly reproduced, accurate, and easy to understand. The text contains little more than a complete account and explanation of the illustrations, and consequently the book can only be regarded as a very clear neurological atlas and cannot replace one of the larger textbooks. Except for an occasional reference to the function of certain tracts, the work is only concerned with structure.

Both the authors and the publishers are to be heartily congratulated on producing one of the most serviceable and useful neurological atlases yet seen.

# THE LYMPHATIC DRAINAGE OF THE HEART

## (*A preliminary communication*)

By L. R. SHORE, M.A., M.B., M.R.C.P.

EXAMINATION of the literature shows that the accounts of the lymphatic system of the heart differ very widely, both of the glands into which lymph vessels drain from the heart and of the disposition of the main lymphatic collecting vessels themselves. I have studied the lymphatic system of the heart of the sheep and of the rabbit, and some preliminary observations are made on the human. The results are set out in this preliminary communication in the hope that the attention of clinicians and morbid anatomists may be directed to the lymphatic glands in cases of bacterial infections of the heart that may come under their notice.

### 1. THE SHEEP

*Method.* Sub-epicardial injections of Prussian blue (prepared according to the formula of Jamieson and Dobson) were made with a fine hypodermic needle into the dead heart. Flow along a main collecting lymph vessel was very obvious when a tributary was punctured and it was facilitated by centripetal massage. The arrangement of the lymphatic vessels was found to fall into two types, which may be called types I and II. The main collecting trunks are *anterior* and *posterior*, and it is in respect of the posterior collecting trunk that types I and II differ.

*Anterior collecting trunk.* Fig. 1 shows the general disposition of lymphatic vessels revealed by a few injections near the apex of the heart. The main anterior collecting trunk is formed on the left side of the root of the aorta, just in front of the origin of the left coronary artery, and runs up in the interval between the pulmonary artery and aorta in a sub-epicardial mass of fat; its tributaries are very numerous and converge to the root of the left coronary artery by vessels from the right ventricle which run in the right part of the auriculo-ventricular groove, and others running upwards from the front of both ventricles to the same point. The areas of the sheep's heart supplied by the two coronary arteries are shown in fig. 6, and these may be compared with the areas of lymph drainage shown in figs. 1 and 2. It is seen that there is no correspondence between the drainage areas of the main lymphatic trunks and the distribution of the main branches of the coronary arteries, other than that certain lymph vessels lie near the arteries in the inter-ventricular and auriculo-ventricular sulci. The lymph drainage of the anterior trunk includes the whole of the front and most of the back of the right ventricle, as is shown in figs. 1 and 2.

*Posterior collecting trunk. Type I.* Fig. 3 shows that the vessels from the back of the left ventricle and margo obtusus run to a vessel lying in the left part of the auriculo-ventricular groove. This vessel runs to the right and

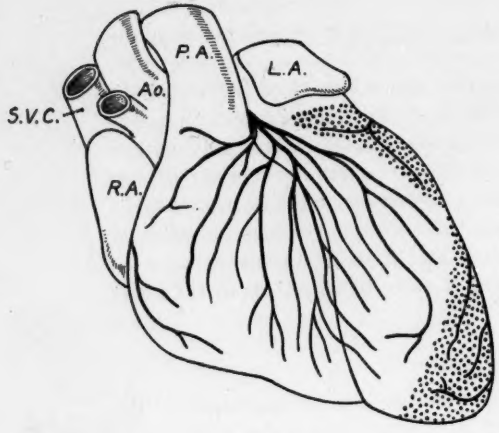



Fig. 1.

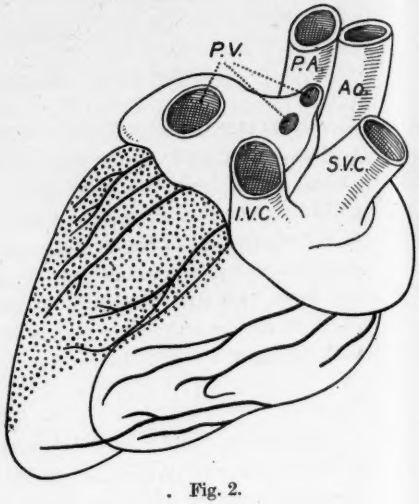



Fig. 2.

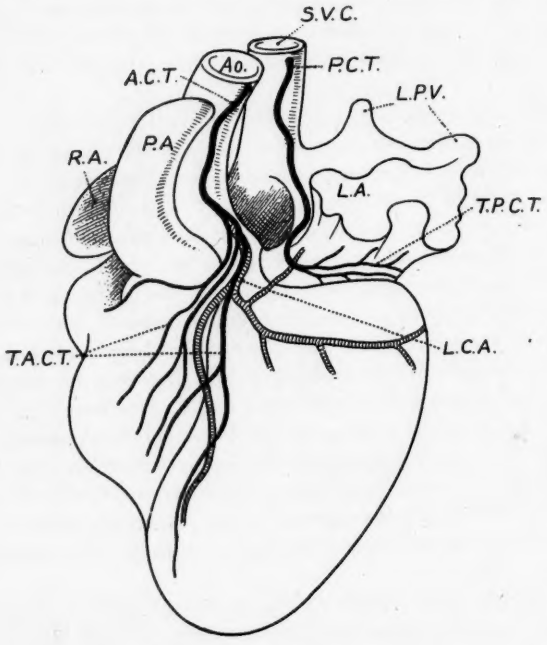



Fig. 3.

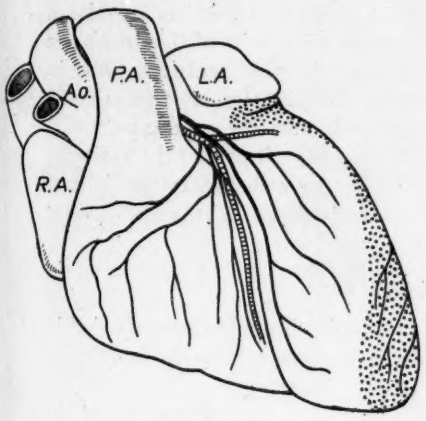



Fig. 4.

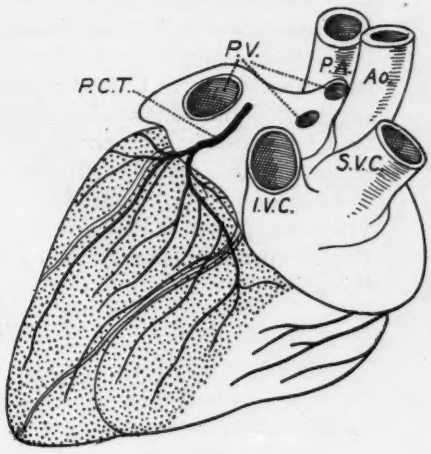
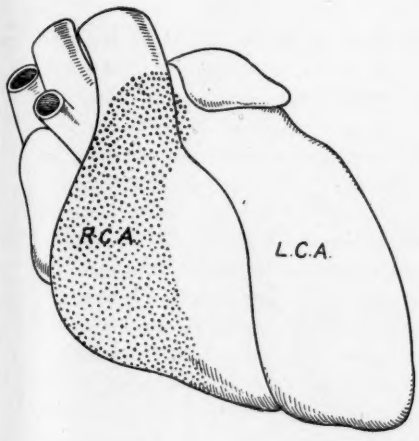



Fig. 5.



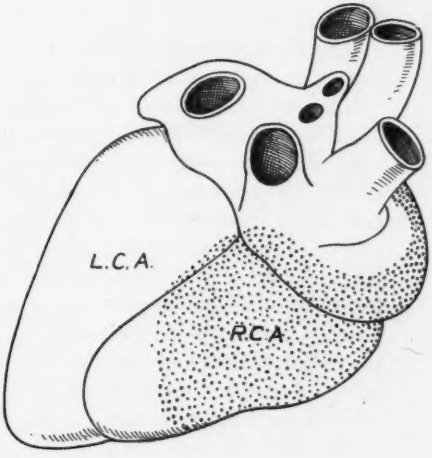




Fig. 6.

forwards, closely applied to the anterior surface of the left auricle, where it lies in the posterior wall of the transverse sinus of the pericardium, after which it takes a vertical course on the antero-medial surface of the superior vena cava. The termination of this trunk is, as yet, undetermined.

*Posterior collecting trunk. Type II.* Fig. 5 shows that this trunk drains a larger area than type I. In the specimen figured tributaries of this trunk are seen to drain an additional area on the back of the *right* ventricle, while in type I the area is approximately limited by the posterior inter-ventricular sulcus. The drainage area on the anterior surface is much the same as in type I. Tributaries converge to a trunk which runs from the left part of the auriculo-ventricular groove to the back of the left auricle, immediately to the right of the left inferior pulmonary vein. This trunk has not yet been traced beyond this point.

## 2. THE RABBIT

*Methods.* The lymphatic drainage of the rabbit's heart has been studied in two ways: (1) Indian ink injection; (2) observations on rabbits the subjects of experimental endocarditis.

*Method* 1. Indian ink was injected into the ventricular myocardium of the living rabbit and search made for lymphatic glands containing pigment. By steadying the heart for a few moments with the fingers it was not difficult to inject the left ventricle, but the small size of the animal and the thinness of the right ventricle made it difficult to do the same on the right side. As a result of dissection of the thoracic viscera of five rabbits the following results may be stated:

(*a*) *Lymphatic glands.* A *constant* gland lies between the right superior vena cava and ascending aorta and in front of the right branch of the pulmonary artery. In figs. 7 and 8 I have sketched a case in which the gland was double; it seemed that there was some difference in the afferents to the two glands. In one rabbit an additional gland containing pigment was found on the back of the left bronchus, as depicted in fig. 9. I recently had the opportunity of examining the viscera of a rabbit in which a 1 in 50 suspension of carmine in saline had been injected into the pericardium 18 hours before death. The gland referred to above, near the right superior vena cava, contained pigment; no other gland containing pigment was found. The inference is that the gland between the right superior vena cava and the ascending aorta receives the lymph from the pericardium as well as from the substance of the heart.

(*b*) *Superficial lymph vessels and collecting trunks.* As in the sheep it was possible to identify anterior and posterior collecting trunks. The anterior trunk resembles that found in both types in the sheep. The *posterior* collecting trunk in the rabbit differs from both types in the sheep. It passes from the back of the left ventricle into the left part of the auriculo-ventricular sulcus and then to the right in the *anterior* wall of the transverse sinus of the pericardium; thence it inclines upwards parallel to and slightly behind the anterior

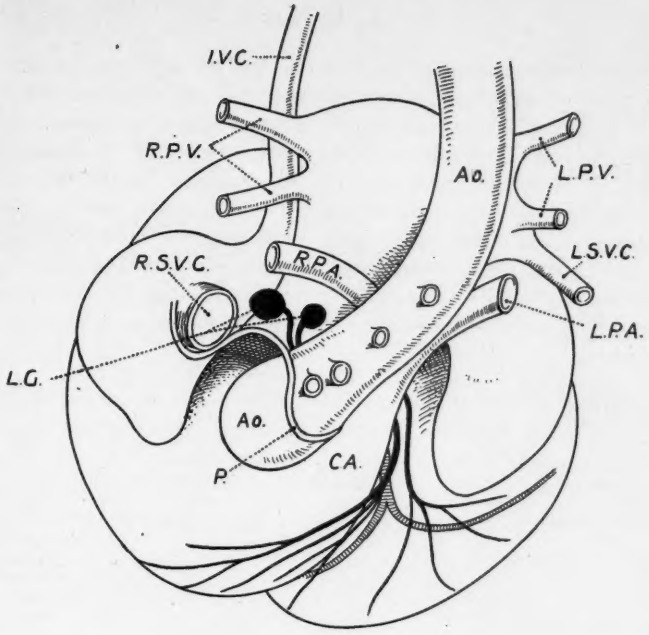



Fig. 7.

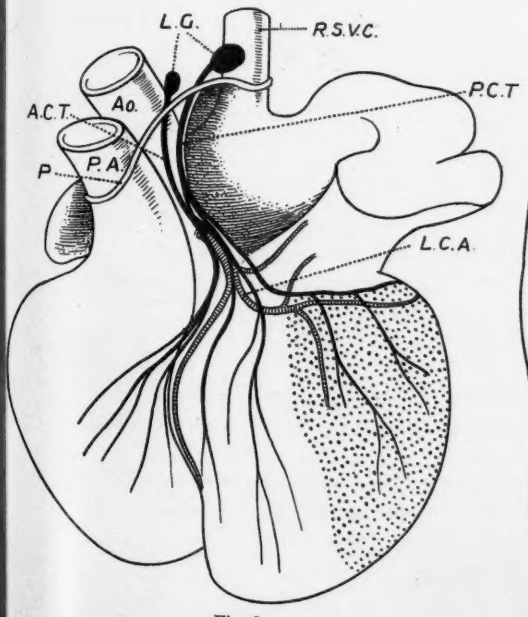



Fig. 8.

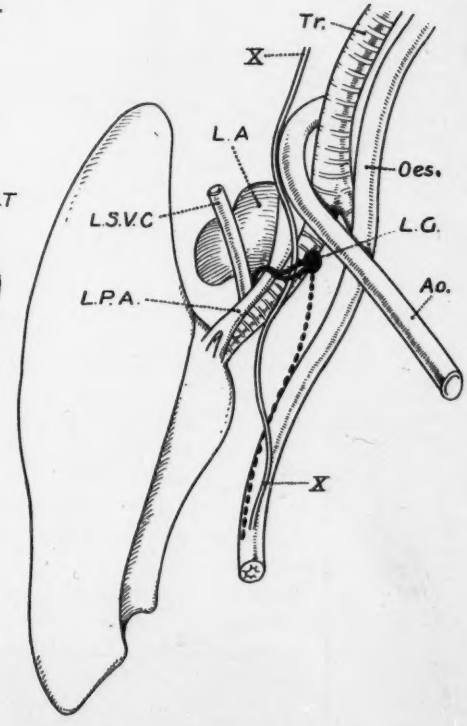



Fig. 9.

collecting trunk, as shown in figs. 7 and 8. In four of the five rabbits the two glands shown in figs. 7 and 8 were merged into one; this specimen is figured as it shows the termination of the two separate collecting trunks.

*Method* 2. Observations on rabbits the subjects of experimental endocarditis. Dr Mervyn Gordon has very kindly given me the opportunity of examining the thoracic viscera of four rabbits inoculated intravenously with micro-organisms for the production of endocarditis. I have recorded the position of enlarged glands and endeavoured to correlate them with the pathological lesions found. The observations are set out in the form of a table which includes the rabbits injected with Indian ink and those with experimental endocarditis.

*Table showing position of glands affected in the rabbit as a result of* (1) *Indian ink injection;* (2) *endocarditis of bacterial origin.*

| | Right superior caval group | | Below arch of aorta | Paratracheal | | Left superior caval group | | Left para-bronchial | |
|---|---|---|---|---|---|---|---|---|---|
| | Medial | Lateral | | Right | Left | Ant. | Post. | | |
| 1. | + | . | . | . | . | . | . | . | Experimental injection of Indian ink into the substance of the ventricle |
| 2. | + | . | . | . | . | . | . | . | |
| 3. | + | . | . | . | . | . | . | . | |
| 4. | + | . | . | . | . | . | . | . | |
| 5. | + | . | . | . | . | . | . | + | |
| 6. | + | . | + | . | . | . | . | . | Carmine injected into pericardium. Gland in arch of aorta not pigmented |
| 7. | + | + | + | + | . | . | . | . | Multiple abscesses. Vegetations mitral and tricuspid valves |
| 8. | + | + | . | + | + | . | + | . | Vegetations tricuspid valve and abscess L. vent. |
| 9. | + | + | . | . | . | + | . | . | Early vegetations mitral valve |
| 10. | + | + | . | . | . | + | . | . | Vegetations mitral and tricuspid valves |

Details relating to the rabbits in which endocarditis was induced:

Rabbit 7. Figs. 10 and 11. *Streptococcus pyogenes.* Multiple abscesses of myocardium. Mitral and tricuspid vegetations.

Rabbit 8. Fig. 12. *Strept. pyogenes.* Abscess left ventricle. Vegetations on tricuspid valve.

Rabbit 9. Fig. 13. *Strept. pyogenes.* Early vegetations on mitral valve.

Rabbit 10. Fig. 14. *Strept. faecalis.* Large vegetations on mitral and tricuspid valves.

It will be noted from the table that the gland near the right superior vena cava is constantly affected. There is no indication of the lymphatic drainage of *individual* cardiac valves in respect of particular lymph glands.

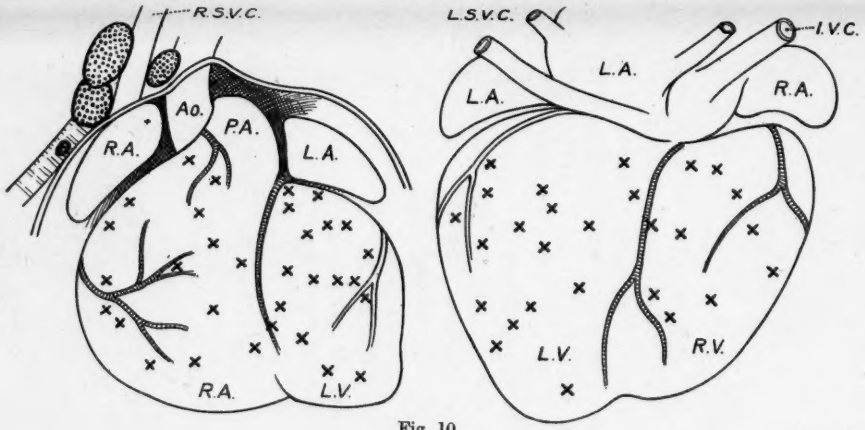



Fig. 10.

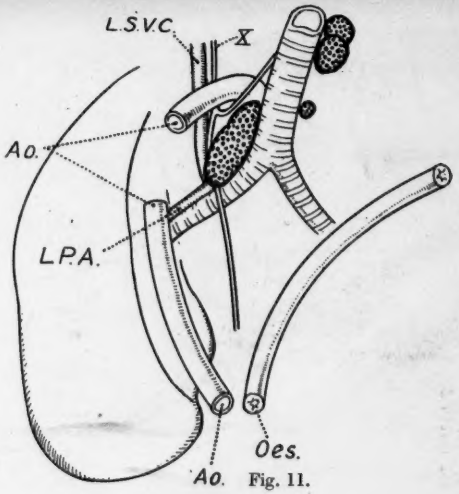
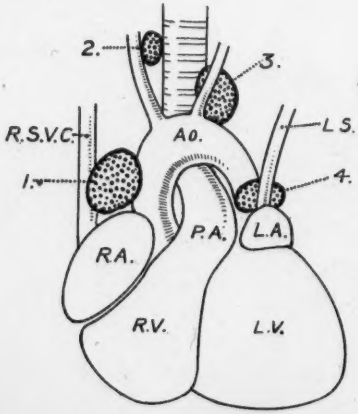



Fig. 11.



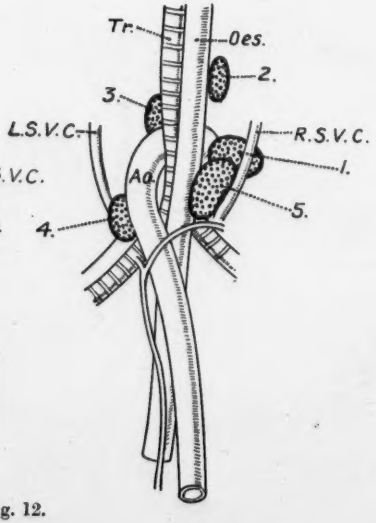




Fig. 12.

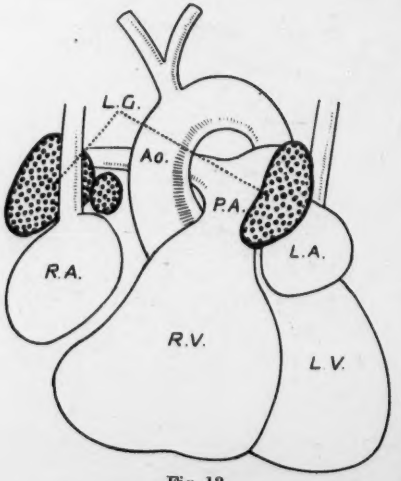



Fig. 13.

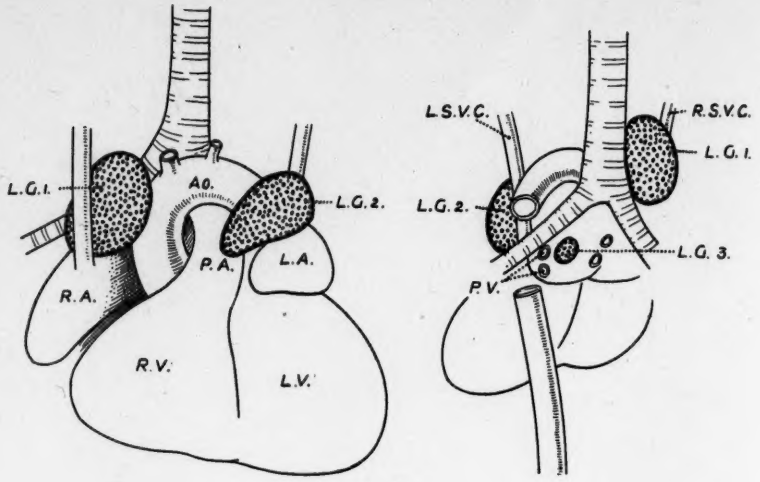



Fig. 14.

### 3. THE HUMAN

Special search has been made for lymphatic glands in the positions suggested by the study of the lymphatic system of the sheep and rabbit. A preliminary search in the post-mortem room in connection with a case diagnosed in life as infective endocarditis, showed the following glands enlarged (fig. 15): (1) near the superior vena cava; (2) on the back of the left auricle to the right of the left inferior pulmonary vein.

The presence of a gland between the superior vena cava and ascending aorta and in front of the right branch of the pulmonary artery, recalls the gland found with such constancy in a similar position in the rabbit. The gland by the left inferior pulmonary vein recalls the disposition of the type II posterior collecting trunk in the sheep. I propose to name these glands as follows: the gland that lies outside the pericardium, in the area defined by the superior vena cava, ascending aorta and right branch of the pulmonary—*the caval gland of the heart*; that which lies outside the pericardium, to the right of the left inferior pulmonary vein—*the auricular gland of the heart*. By the use of a precise nomenclature it is hoped that descriptions of post-mortem specimens may be facilitated.

In the description of human material from the post-mortem room some emphasis is laid on the colour of the gland. A gland deeply pigmented with soot is suggestive of a connection with the bronchial system. Post-mortem observations as yet have been very few, but the following are of interest:

Case 1 (fig. 15) shows both caval and auricular glands enlarged. The auricular gland was about one and a half inches distant from the nearest black

bronchial gland, and it was not pigmented. There was endocarditis of both mitral and tricuspid valves.

Case 2 (fig. 16) shows caval and auricular glands enlarged. The auricular glands were multiple, fleshy and contrasted with a deeply pigmented gland (presumably of the bronchial system) that lay just below the left pulmonary veins. Endocarditis of the mitral valve was present.

Case 3. In a case of mitral disease of very long standing and extreme narrowing of the mitral orifice, a hard fibrous caval gland was found.

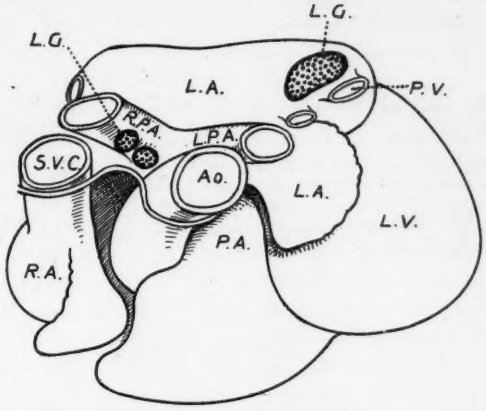



Fig. 15.

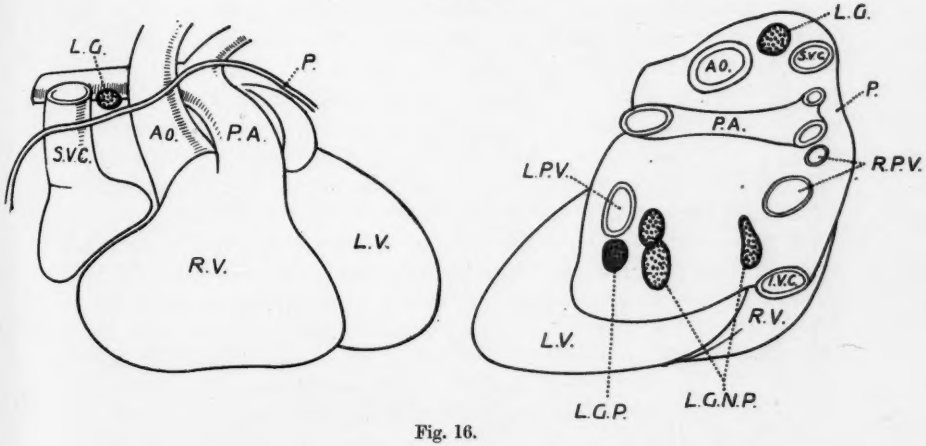



Fig. 16.

This communication contains the data I have gathered up to the present on the lymphatic drainage of the heart, and I propose to continue investigations in the post-mortem room and laboratory. As yet, I have had no oppor-

tunity of making a direct injection of Prussian blue into the caval or auricular glands of the foetus, nor have I attempted to describe the microscopic appearance of the lymphatic vessels.

I wish to express my cordial thanks to Professors Elliot Smith and Lovatt Evans who have given me facilities for work in University College, London, and much helpful advice; also to Dr Mervyn Gordon for the material he has placed at my disposal. To Dr Francis Davies I owe my best thanks for assistance at all stages of this investigation, for presenting this paper in my absence and for many other acts of friendship.

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# ON THE PRESENCE OF A SERIES OF ECTODERMAL PLACODES IN THE HEAD REGION OF A SPARROW EMBRYO

By FRANK GOLDBY, B.A. (Cantab.)
*Formerly "Frank Smart" Student of Gonville and Caius College*

The following observations were made while working in the Embryological Laboratory of the Anatomy School in Cambridge under the direction of Prof. J. T. Wilson in 1924, during the tenure of a Studentship in Gonville and Caius College.

The specimens were shown at the May meeting of the Anatomical Society of Great Britain and Ireland in Sheffield in that year, and a brief description appeared in the *Proceedings* of the Society for May 1924, p. 104. The main object of this paper is to furnish illustrations of the structures in question.

The observations were made upon a series of transverse sections of a sparrow embryo of a stage corresponding roughly to that of a chick embryo of about 40 hours. The series was incomplete at the caudal end of the embryo and unfortunately the histological condition of the specimen was not entirely satisfactory, so that it was impossible to ascertain with precision the possible underlying neural relationships of the placodes. Nevertheless, the actual structural features presented by the members of this extraordinary series of epidermal placodes are so clearly and definitely marked, and their occurrence in an amniote represents such a striking and unprecedented phenomenon, that it seems worthy of special attention and record.

The placodes in question are small areas of more or less columnar ectodermal cells situated in a dorso-lateral position along the head. They appear definitely to lie in series with the auditory placode, two of them being caudal to it and the others more cranially (rostrally) placed. Not the least extraordinary fact concerning them is that they are present only on one side of the head. Their relative positions—and also their relative sizes—are roughly indicated in the diagram in fig. 1, founded upon Lillie's diagram of the head region in a 40-hour chick embryo.

The placodes may be described individually as follows:

Placode I (fig. 2). This consists of a well-defined and sharply cupped placode consisting of cuboidal cells which are distinctly larger than the cells of the neighbouring epidermis. It is situated alongside the mid-brain region about its middle. Underneath it lie a number of cells which can be traced along the side of the mid-brain towards its rostral limit. These cells may possibly

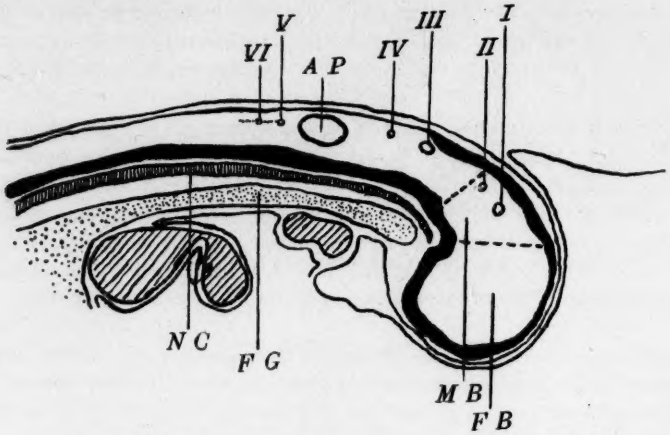
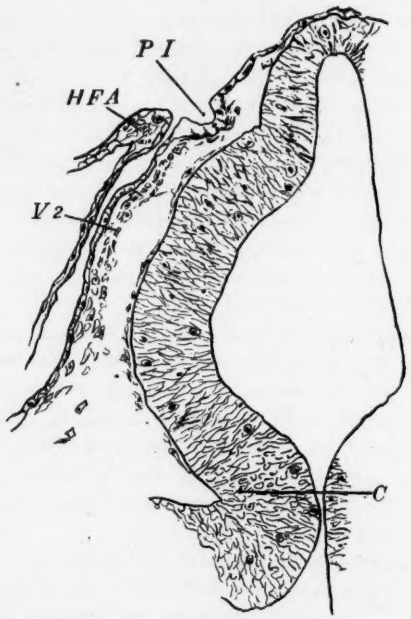



Fig. 1. Median sagittal section of a 40-hour chick embryo (slightly modified from Lillie). *A P*, auditory placode; *F B*, fore-brain; *F G*, fore-gut; *N C*, notochord.




Figs. 2–5. Transverse sections across head of sparrow embryo of a stage corresponding to fig. 1. *C*, constriction between fore-brain and mid-brain; *D A*, dorsal aorta; *F G*, fore-gut; *H F A*, head fold of amnion; *P* I–VI, placodes I–VI; *S* I, cranial end of first somite; *V C L*, vena capitis lateralis; *V* 2–3, trigeminal neural crest tissue.

represent the ophthalmic division of the trigeminus. There is no evidence of any proliferation of cells from the placode joining this group of cells.

Placode II. This lies close to the caudal boundary of the mid-brain. It is much smaller than placode I, but otherwise it is very little different. No special cell-group underlies it.

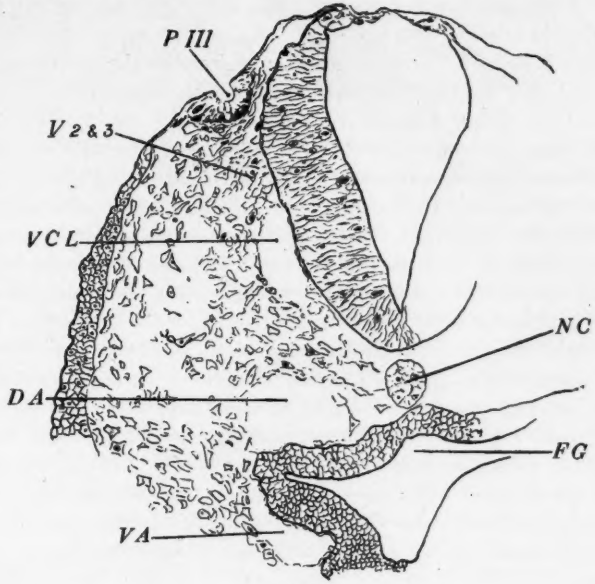



Fig. 3.

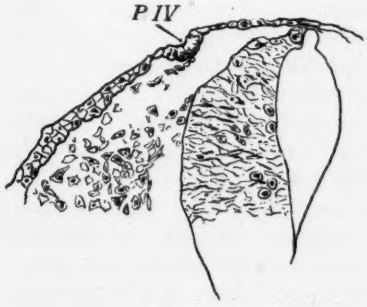



Fig. 4.

Fig. 5.

Placode III (fig. 3). This placode lies cranially to the first visceral pouch. It is the largest of the series and, like the first, it is sharply cupped. The concave placode consists of well-marked columnar cells sharply defined basally. Be-

neath it lies a cell-proliferation which may represent a portion of the trigeminal neural crest. Yet here again there does not appear to be any morphological relation, other than contiguity, between the placode and the presumable crest-cells.

Placode IV (fig. 4). This small but quite distinct placode also lies just anterior to the first visceral pouch. There is no evidence of any ganglionic proliferation in relation with it.

Placodes V and VI. These, although in series with the others, lie caudal to the auditory placode. They are smaller and less well-formed than the anterior members of the series. Placode VI is fairly definite (fig. 5). It lies opposite the cranial end of the first somite. (In the earlier note in *Proc. Anat. Soc.*, 1924, p. 104, this placode was erroneously described as lying lateral to the ganglion of the IXth nerve. In that note also a different mode of designation was employed for the placodes.) Placode V lies above the second visceral pouch. It is the only one of the series about which there can be any real doubt. It is both small and indefinite and might possibly be only an artificial indentation, though it is believed to be a rather imperfectly formed member of the series.

The sectional series further affords some indication that placodes V and VI form portions of a ridge of somewhat thickened ectoderm extending from placode V caudally through the VIth and becoming lost a few sections further on. It is however not very well marked, nor quite continuous, and its existence would require confirmation in better material.

Except in its much larger size the auditory placode does not differ markedly from the placodes above described. Its constituent cells, however, cannot be distinguished so clearly, though this is probably only due to more active proliferation.

According to their position the placodes might be classified, as in the former note, as follows:

| | |
|---|---|
| Premandibular | Placodes I and II. |
| Mandibular | Placodes III and IV. |
| Hyoidean | The auditory placode and possibly placode V. |
| Branchial | Placode VI. |

But any real morphological relation to the arches of the head or even to the ganglia is very questionable. The facts that (*a*) the placodes are unilateral in this, the single observed case, that (*b*) they exhibit such irregularity in size among themselves, and (*c*) that so far as can be seen they correspond to no adult structure, all suggest that they are vestigial in character. Their general position, and their arrangement in obvious series with the auditory placode, give colour to the further suggestion that they represent traces of the acousticolateral system of anamniota.

In conclusion I wish to express my gratitude to Prof. Wilson for the help and advice which he has given me. My thanks are due also to Mr Walter Calcott, from whose photomicrographs the illustrative figures were traced.

# THE PLURIOVULAR FOLLICLE, WITH REFERENCE TO ITS OCCURRENCE IN THE FERRET

By D. MAINLAND, M.B., Ch.B.,
*Demonstrator of Anatomy in the University of Edinburgh*

One hundred years ago von Baer (1827) referred to his observations of pluriovular follicles in the ovaries of the dog and the pig. Recently was published Hartman's paper (1926), partly devoted to these follicles as they occur in the opossum. During the century which included these two dates, over sixty publications appeared, recording the finding of, or the search for, the abnormality in Mammals. To obtain data for a comparative study, analysis of very nearly all of these is here made, and certain of the data have been selected to form a brief historical summary, arranged according to: year of the publication in which the record is to be found; author; animal. An asterisk denotes a record of "tubes" containing ova.

1827: v. Baer (dog, pig); 1840: Hausmann (dog); 1842: Bidder (cow), Bischoff (rabbit); 1845: Bischoff (dog); 1861 and 1863: Klebs (man); 1863: Grohe (man), Pflüger* (cow, cat, dog, man), Quincke (man, cat, rabbit, cow), Schrön (cat, dog); 1867: Kölliker (man); 1869: Plihal* (cow, man); 1870: van Beneden (man, kangaroo), Slavjansky (man), Waldeyer (man, dog); 1874: Foulis (general: cow, cat, man were chiefly studied); 1875: de Sinéty (dog, cat); 1878: Balfour (rabbit); 1879: Balbiani (dog); Wagener (rabbit, dog); 1880: van Beneden (bat); 1881: Schulin (sheep, pig, cow, bat, man); 1887: Janosik (general: cat, dog, man; rabbit specifically); 1888: Nagel (man); 1891: Alexenko (man); 1893: Klien (man), Schottländer (man); 1895: Hellin (man; reference also to findings of Hensen, Kiwisch and Scanzoni, without detail); 1898: v. Franqué (man); 1899: Stöckel (man), Rabl (man); 1900: Bouin, P. and M. (dog), v. Schumacher and Schwarz (man); 1901: Honoré (rabbit), Loeb (guinea-pig), Rosner (armadillo); 1903: Ancel (dog), Cuénot (armadillo); 1905: Schottländer (man); 1907: Welch (man); 1908: Smyth (dog); 1908–9: v. Winiwarter and Sainmont (cat); 1909: Chappelier (mouse); 1911: Schmaltz (dog, pig, sheep); 1912: Arnold (man), Hansemann (man), O'Donoghue (*Dasyurus viverrinus*), Tur (cat, rabbit); 1913: Kingsbury (cat); 1915: Corner (pig); 1917: Loeb (guinea-pig); 1921: Häggström (man), Woerdeman (man; reference to findings of Strassman, man); 1924: Allen, Francis, &c. (mouse), Kennedy (dog, cat, rabbit, guinea-pig, fowl); 1926: Hartman (opossum, *Macacus rhesus*, cat, dog).

The analysis has revealed in many instances a lack of standardisation. A few observers have, in individual ovaries, estimated the proportion

of pluriovular follicles (Rosner, 1901; Cuénot, 1903; O'Donoghue, 1912; Häggström, 1921). The more important question of the frequency with which ovaries containing pluriovular follicles are met in a series of ovaries has also rarely been adequately answered. Such observations have been made by Schrön (1863: 400 ovarian "Präparate" of cat; 80 of dog), O'Donoghue (1912: serial sections of ovaries of 45 individuals of *Dasyurus viverrinus*), Patterson (1913: over 50 pairs of ovaries of Texas armadillo), and by Hartman (1926: ovaries of about 150 opossums). The widespread distribution of the pluriovular follicle in Mammalia is obvious; of its frequency in the different species we are still largely ignorant, and the possible relationship to twinning or to fertility in general is, in regard to many species, obscure.

After the example set by Hartman (1926) in his extensive observations, it seemed desirable to make a survey of another Mammal, a member of the group Carnivora—the common ferret, for which, apparently, no record of the abnormality has hitherto been published.

## MATERIAL AND METHODS

In the present survey, 496 ovaries of adult ferrets were used, and 39 ovaries of young, i.e. non-mature, ferrets[1]. The animals had in most instances been killed by chloroform vapour; a few by coal-gas. The ovaries had been fixed immediately after death by one or other of the following fluids: strong Flemming, Lenhossek, Mann's picro-corrosive sublimate, Maximow, Perenyi, Zenker. Each ovary was cut as a complete series of paraffin sections at 10 or 7 microns. In most cases both ovaries from an individual could be examined. The stains employed were chiefly Mayer's haemalum and eosin, Heidenhain's iron-alum haematoxylin, Mallory's connective tissue stain. Heidenhain's "Azan" stain, and the picro-Ponceau S stain of Curtis have also been used.

As the adult animals were purchased for breeding from dealers, no information concerning the exact age could be obtained. In the following records, unless it is specially indicated that a statement refers to the ovaries of non-mature animals, the implication is that adults only are referred to.

Before the results of the present observations are studied, it is desirable to indicate the limits of the term "pluriovular" as here employed. I do not apply the term to those follicles which differ from the normal merely by the presence of other follicles in their thecae. This exclusion appears from the literature to be traditional. Hartman (1926) further objected to the inclusion of primordial follicles in the group, for these might or might not become pluriovular follicles. In the present numerical survey, I have excluded primordial follicles in which the ova are in contact or are separated by only a single layer of epithelium between their adjacent surfaces, unless the epithelium passes from the non-adjacent side of the one ovum to that of the other without leaving a gap or groove externally.

[1] The material used is the property of the Department of Anatomy, Edinburgh University.

In order to obtain a number of pluriovular follicles for systematic comparison, a survey of the collection of adult ovaries was first made. At the same time an attempt was made to form an estimate of the frequency of the condition. Groups of the different ovaries were formed by random choice, and each ovary in a group was subjected to the same type of examination.

## RESULTS OF THE SYSTEMATIC EXAMINATIONS

A. Thirty-nine ovaries from 21 different animals. From each ovary two or three slides were examined, situated at equal intervals in the series. The numbers of sections examined averaged approximately one-tenth of the total.

Ovaries found to contain pluriovular follicles: 13.

Number of animals in which the follicles were found: 8.

Number of pluriovular follicles found: 25.

Maximum in any one ovary: 4 (two instances).

Maximum in any one animal: 6 (two instances).

B. Fifty-eight ovaries, probably from rather more than half that number of animals. (It was not possible in all cases to pair off the ovaries according to the animals to which they belonged.) Two methods were employed on the same ovaries.

Method I. From each ovary 10 follicles of volume about ·00016 c.mm. or over were examined from end to end. Those chosen were the first ten complete follicles of proper size met when the examination commenced at one end of the series of sections. The smallest of these possessed epithelium which had almost entirely passed from the early flat condition to the later cubical; the larger follicles were such as might reveal themselves as pluriovular only when traced through the series containing them.

Of the 580 follicles, 9 were pluriovular, from 8 different ovaries, i.e. about 1·5 per cent. of the follicles examined.

Method II. From each ovary 10 sections were examined minutely. The intervals between them were chosen so as to be as nearly equal as was practicable. The sections examined amounted on the average to about one from every 40.

In the 580 sections, 33 pluriovular follicles were found, from 19 different ovaries. This was, very roughly, 0·1 per cent. of the follicles examined. The difference in this percentage from that of Method I, is largely due to the fact that in the latter primordial follicles were not observed, and that the sections examined were in series.

Maximum number of pluriovular follicles found in one ovary by Methods I and II: 4 (two instances). (In only one instance was a follicle recorded under both headings.)

In Examinations A and B II, conducted on different ovaries, the ovaries found to contain pluriovular follicles were about one-third of those examined.

The remaining ovaries were examined less minutely than the preceding, but a number of pluriovular follicles were recorded in them, and there appeared

no reason to conclude that they differed in respect of the frequency of these structures from those more minutely examined.

### COMPARISON OF PLURIOVULAR FOLLICLES

By these various methods, 154 pluriovular follicles were noted From them, 100 were chosen for examination, so that impressions gained in the previous survey should be verified or corrected. Complete follicles and those best preserved were selected; the choice was spread widely among the ovaries containing the specimens. Notes were made under the following headings: Stage of the sexual cycle in the animal; Number of corpora lutea, if the animal was pregnant; Position of the follicle in the ovary; Shape of the follicle; Size in cubic millimetres; Presence or absence of liquor folliculi; Follicular epithelium,—the number of layers and the shape of the cells; Degeneration in the follicular epithelium; Number of ova in the follicle; Degeneration of ovular nucleus or cytoplasm; Relative sizes of the ova; Position of the ova in the follicle and relationship to each other.

### THE SPECIES DISTRIBUTION OF PLURIOVULAR FOLLICLES

As already indicated, generalisations concerning the frequency of the condition in ovaries of different species are not numerous. From a survey of the literature it appears that only the following conclusions are justified. Among Marsupials, the opossum presents the condition very frequently. It was found by Hartman (1926) in approximately two-thirds of the preparations he examined (ovaries from about 150 opossums). In another Marsupial, *Dasyurus viverrinus*, it does not seem to be frequent (O'Donoghue). In Eutherian Mammals of the Edentate group, its rarity in the Texas armadillo seems to have been established (Patterson, 1913). As regards Ungulates, the most satisfactory evidence is that based on the wide experience of Corner, who was led to conclude that in the pig the pluriovular follicle is uncommon (1915 and 1923). The view of Schmaltz is somewhat different, probably owing to less abundant material, possibly owing to some differences in the breeds of animals surveyed.

The extent to which some of the genera of Rodents are used for ovarian research, together with the infrequent appearance of reports upon the pluriovular follicle in their ovaries, might be thought to indicate the rarity of the phenomenon in this group. The common attitude of slight interest in the subject may, however, possibly be indicated by the illustration of one such follicle in the mouse ovary, shown by Allen, Francis, and their co-workers during discussion of another subject. Regarding Carnivores, on the other hand, there seems to be a fair consensus of opinion that the dog ovary frequently presents pluriovular follicles (Waldeyer, Balbiani, Ancel, Schmaltz). The only dissentient seems to be Schrön. There seems to be little evidence concerning the ovary of the adult cat in regard to the frequency of the phenomenon. The present investigations have indicated that in the adult ferret the condition is met with moderate frequency; but pluriovular follicles are seldom,

perhaps never, abundant in any ovary, relative to the normal follicles. In Chiroptera, it is of interest to note that van Beneden (1880) stated that the horseshoe bat presented pluriovular follicles more commonly than *Vespertilio murinus* did.

Although a fair number of individual human ovaries containing pluriovular follicles are on record, evidence of the frequency of the condition in the human ovaries is still not abundant. Welch instituted enquiries among many histologists and pathologists; their opinions agreed with that of Waldeyer (mentioned by v. Franqué) indicating the rarity of this follicular abnormality in human (presumably adult) ovaries.

Paucity of data prevents any extensive correlation between the species distribution of this condition and that of other phenomena; but such comparisons as are possible are of some value as introductory to the more fruitful study of individual instances.

## CONCOMITANT PECULIARITIES OF OVARIAN STRUCTURE

### (*a*) *Plurinucleated Ova*

It has been held by some authors, working with young ovaries, that the multiple nucleus is a precursor of the pluriovular follicle (Quincke; Klebs, 1861 and 1863; van Beneden, 1870; Balfour and Eismond inclined to a similar view). In adult human ovaries apparent stages of transformation from the former condition to the latter have been observed by Stöckel, Rabl, and v. Schumacher and Schwarz. Unfortunately our knowledge of the frequency of plurinucleated ova is as unsystematised as that of the frequency of pluriovular follicles. There is co-existence of the two conditions in the opossum ovary, in which plurinucleated ova are very frequent (Hartman, 1926). In the dog ovary there seems to be no evidence of this frequency. Von Winiwarter and Sainmont recorded the presence of both the follicular and the nuclear abnormality in the ovaries of very young cats. Criticism of this as a suggested mode of origin of pluriovular follicles has been advanced by a number of authors. Bischoff (1863) did not believe in the existence of plurinucleated ova. Waldeyer opposed Klebs' contention that egg division took place in follicles after their separation as such. Observation of individual ovaries from various species of animals, containing numbers of pluriovular follicles, has shown no evidence of association with plurinucleated ova (P. and M. Bouin, Honoré, Arnold, O'Donoghue, Hartman, 1926—a cat specimen).

The present investigations were commenced with the object of ascertaining the frequency of plurinucleated ova in the ferret, as well as of studying the pluriovular follicle; but careful scrutiny of thousands of ova in the adult has failed to reveal an instance of this nuclear abnormality. The series of ovaries from young animals is much more limited, but here also no evidence appears that multiple nuclei in the ova are connected with the formation of the abnormal follicles.

### (*b*) *Abundance of Small Follicles*

Even in the anoestrous period, the opossum ovary contains a very large number of small follicles (Hartman, 1923). Individual cases in which pluriovular follicles were accompanied by an abnormal abundance of small follicles have been reported by v. Franqué (human), v. Schumacher and Schwarz (human), and Hartman (1926, cat). In the ferret, follicles of various sizes are to be found in the ovaries abundantly at all periods of the year, and I am not prepared to correlate any abnormality in this respect with the presence or absence of pluriovular follicles.

### (*c*) *Epithelial Ingrowths*

Tube-like ingrowths of the germinal epithelium form a marked feature of the ovary of the dog (Waldeyer, Balbiani, Schmaltz). Hartman (1926) compared these to the "primordial egg masses" found in the opossum. (Balbiani, however, stated that in the dog they often contain no ova.) A further comparison is made by Hartman (1926) with the structures found in the ovary of an 18-year-old girl by Plihal, and diagnosed by him as persistent Pflüger's tubes. Individual instances of the co-existence of pluriovular follicles and epithelial ingrowths have been noted by v. Schumacher and Schwarz (adult human) and by Woerdeman (human, probably adult).

The ferret ovary contrasts with that of the dog in possessing a tunica albuginea that forms a definite narrow band lying close beneath the germinal epithelium. Where strands of ova and epithelium extend inwards from near the free surface, their admixture with spindle cells and fibrils is as a rule intimate. Tube-like ingrowths are rare. In the adult ferret ovary I have not found that pluriovular follicles are associated with abnormally numerous epithelial ingrowths or with follicular strands; but, as will be indicated later, it appears that the production of the abnormal follicle is dependent on the relationship of follicular tissue to connective tissue at this very early stage of follicular development. This question of ingrowths is, in fact, merely a part of the larger question now to be treated.

## THE RELATIONSHIP OF THE OVARIAN CONNECTIVE TISSUE TO THE FOLLICLES

Two chief types of opinion have been held concerning the mode of action of the connective tissue in the production of pluriovular follicles:

(*a*) Secondary union of follicles owing to weakness of intervening connective tissue;

(*b*) Primary disproportionate development of the follicles and the connective tissue.

(*a*) *Secondary Union.* Three suggestions have been made concerning the sizes of the follicles concerned.

(1) Union during enlargement of primordial follicles suggested by Grohe. In the ferret ovary, two follicles of about primordial size are frequently seen close together, separated only in part by connective tissue, and in any single instance it is not obvious whether this tissue is penetrating or being expelled. The former alternative is favoured by our knowledge of the general tendency of the cells of this tissue to penetrate, and especially by the demonstration of that tendency kinetically by tissue-culture experiments. (See, for example, Fischer, p. 117.) The actual frequency with which the partial separation is seen, compared with the frequency of pluriovular follicles, indicates that invasion is proceeding in the vast majority of cases.

(2) Union of medium-sized or large follicles. Rosner published figures to represent stages in a supposed union of follicles larger than primordial, even containing liquor folliculi. In the ferret it frequently happens that two follicles are pressed closely together, and then the follicular epithelium and thecal interstitial cells become much flattened. I have, however, not found stages in which this was followed by breakage of the intervening connective tissue, and consequent union of follicles. Rosner cited lobulation of pluriovular follicles in support of his contention. In the series I have examined some tendency to lobulation is present in follicles without liquor folliculi and containing a larger and a smaller ovum; the smaller forming a projection. This appears explicable by the growth of the larger. The internal tension of the smaller ovum would prevent its being flattened out over the surface of its growing neighbour, and it would come to project as a lobule. This suggestion also would account for the thinning of the epithelium over the smaller ovum.

(3) Union of a small with a large follicle. Loeb (1917) discussed the "hypotypical" ovary of a guinea-pig which had been used in underfeeding experiments, had had its thyreoid gland removed and the lobe of another thyreoid engrafted subcutaneously. Pluriovular follicles were formed here, the author claimed, mostly by "concrescence"—a process by which small follicles, especially primordial, pushed their way into larger ones, perhaps even into degenerating follicles. In the ferret I have noted a number of instances of the presence of a small follicle in the theca of a larger one, but I find no evidence that the former ever loses its integrity. In the guinea-pig discussed by Loeb, the thickness of the granulosa surrounding the different eggs in a follicle was stated to accord with the character of the egg, and this was thought to be compatible only with the view of secondary union. Thinning of epithelium over the smaller of two eggs that are close together seems explicable by differences in the rate of growth, as mentioned above in connection with lobulation of the follicles (fig. 1).

(*b*) *Primary Disproportionate Development* of the follicles and the connective tissue. Suggested by Schrön, and considered possible by Balfour. This theory was advocated at greater length by Schottländer (1893 and 1905), who stated that pluriovular follicles resulted from the irregular growth of connective tissue in the formation of follicles from egg balls. Hellin, the Bouins, Honoré,

O'Donoghue, and Hartman (1926) adopted a similar explanation (imperfect subdivision of Pflüger's tubes). It is this lack of balance in development between follicular and connective tissue that appears to account for the pluriovular follicles of the ferret. As the theory has sometimes been advanced without detailed consideration of the actual mechanism, it may be of value to mention five factors which have been suggested by specimens observed in the ovary of the adult ferret.

(1) Rate of growth of ova. Two ova of just beyond primordial size may be seen lying very close together, with their adjacent sides parallel and separated by epithelium that is greatly flattened. It appears that in such cases growth of the ova has been too rapid for them to be accommodated by displacement of neighbouring structures, and the follicles, instead of forming two separate spheres, tend to form a single one, which may be then surrounded by a common layer of connective tissue.

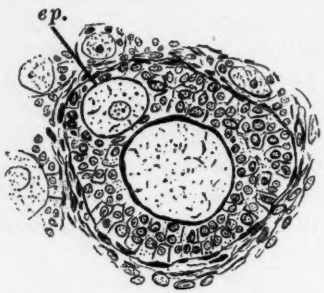



Fig. 1. Two ova in one follicle. The smaller ovum forms a projection, and over it the epithelium, *ep.*, is thin and flat. (× 410.)

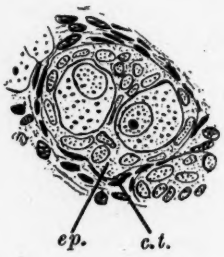



Fig. 2. A stage in the formation of a bi-ovular follicle. The connective tissue, *c.t.*, is excluded from the interovular sulcus by the epithelium, *ep.*, which forms a projection. (× 525.)

(2) Distribution of the follicular epithelium. In the ferret, each primordial ovum is usually surrounded by a single layer of flattened epithelial cells, but, sometimes, only a single layer of epithelium lies between two such ova, and this layer may be very thin, perhaps absent over a part of the surfaces of the ova. This condition is more frequently met than is the small pluriovular follicle, and it therefore appears probable that some other factor is necessary for the production of the latter, even if the single epithelial layer plays a part. Small pluriovular follicles, indeed, frequently show only one layer of flat epithelium between two ova.

(3) Growth of follicular epithelium. The sulcus around the area of contact of two primordial follicles is in some instances filled with epithelium, which may even form a projection outwards instead of the usual depression. Alongside lie connective tissue cells. It appears that these are excluded from the interovular sulcus by the abundance of epithelium (fig. 2).

(4) Slowness of growth or lack of penetrative power of the connective tissue. Evidence of deficient power of the connective tissue was manifested, according to Loeb (1917) by atypical atresia of follicles in the ovary of the guinea-pig, mentioned above, which showed pluriovular follicles. I have not observed such a generalised deficiency associated with pluriovular follicles in the ferret. Factor (3), above, implies a local defect of the connective tissue, at least relative to the epithelium.

(5) Distribution of the connective tissue. In some regions of certain ovaries the connective tissue cells are not so evenly distributed as in other regions. They are arranged in strands along the sides of a row of several follicles, and few at right angles to this, and thus appear less favourably placed than usual for surrounding each follicle before the epithelium of two or more primordial follicles has united to form a common syncytium. In some instances the factor responsible for this distribution seems to be the rate of ingrowth of strands of follicles and epithelium from near the germinal epithelium. Comparison with the ingrowths of the dog ovary is suggested.

Whichever of the suggested factors may be responsible, the essential attainment appears to be an unbroken epithelial surface. There is thus no capillary interval left between the follicles. Instead, there is a capillary interval between the follicular surface and the surface of neighbouring structures; and we may suppose that, under the capillary and surface forces here acting, the young connective tissue cells are compelled to migrate, and thus form the rudiments of a theca common to the epithelium which surrounds the several ova. (For the importance of these forces in the migration of cells, see Fischer, p. 39.)

## THE DEGREE OF THE ABNORMALITY

(*a*) *The Number of Ova in a Follicle.* From previous records it appears that the minimal deviation from the normal number of ova is the commonest—the bi-ovular condition. Records of follicles containing a considerable number of ova have been made: about 10 ova (the Bouins: dog); 12 (Hartman, 1926: *Macacus rhesus*); 13 (Arnold: human); over 100 (Hartman, 1926: opossum; this is exclusive of "egg masses").

The importance of serial sections in an estimation of this kind need hardly be emphasised. From the 100 pluriovular follicles that have been completely examined in ferret ovaries, the following figures were obtained:

Seventy-four follicles each contained two ova; 18 contained three; 2 contained four; 3 contained five; 2 contained six; 1 contained at least 13, probably 14 ova, all of them small. (This follicle showed no liquor folliculi.)

(*b*) *Relation of the Epithelium to the Ova within the Follicle.* Van Beneden (1880) described in the horseshoe bat two types of compound follicle: one in which the follicular epithelium separated the ova; the other in which two or three ova were in direct contact. Both types have been recorded in subsequent publications. The results of the examination of the 100 pluriovular follicles in the ferret may be summarised as follows:

Ova in contact: 37 follicles. Of these, 14 showed the presence of more or less liquor folliculi; in one the liquor had probably been absorbed.

Ova separated by epithelium: 63 follicles. Of these, 38 showed liquor folliculi; in one the liquor had probably been absorbed.

Although the distinction is not of great intrinsic value, the presence or absence of epithelium between two growing ova is important in regard to the theory of origin of the zona pellucida. Foulis (1874) and van Beneden (1880) showed that two ova in contact had developed the zonae pellucidae, just as did ova surrounded by epithelium—an indication that the ovum and not the epithelium was the responsible factor. The observations of O'Donoghue, and of Hartman (1926) support this view, as do some of my own. The other possibilities (migration or degeneration of the epithelium after it had formed the zona) were not considered likely by Hartman (1926). In most cases degeneration can easily be dismissed. To prove that emigration does not occur in any individual instance would be difficult; but the numbers given above, so far as they go, suggest that invasion of the interval between ova occurs as the follicle enlarges, after the zona is at least partly formed, the index of size being the presence or absence of liquor folliculi. Among the more developed follicles, disproportionately more show separation of ova by epithelium than among the less developed. From observation it is clear that the epithelium between ova can undergo great flattening as the ova grow, without losing its continuity; and this suggests that where epithelium does not intervene between ova, it has been absent from the beginning.

In the larger pluriovular follicles that have been described, various degrees of separation of the ova have been noted, from those follicles in which a common cumulus contained two or even more closely apposed ova (O'Donoghue) to those described by Welch and by Smyth, in which the ova lay at widely separated parts of a large follicle. Of the 100 follicles specially examined in the ferret ovary, there were 30 in which the cumulus was observable, either completely or partly formed. In 28, the ova lay in separate cumuli or in cumuli which were in the act of separating (see fig. 5, p. 150).

## THE RELATIONSHIP OF THE AGE OF THE ANIMAL TO THE OCCURRENCE OF PLURIOVULAR FOLLICLES

Among the observations briefly summarised near the commencement of this article, some were concerned with the pluriovular follicle in young animals only. In this category are the records of: Bidder, Klebs, Grohe, van Beneden (1870), Foulis, Nagel, Klien, Hellin, Loeb (1901), Smyth, v. Winiwarter and Sainmont, Chappelier, and Kingsbury.

Klebs (1861) and Grohe emphasised the comparatively great frequency of the condition in the ovaries of young children.

Of the 39 ovaries of young ferrets that have been examined, about three-quarters dated from the earliest days after birth, and showed principally fol-

licles in the process of formation. The remainder were from animals aged from 4 weeks to about 3 months. The animals contributing to this second group were not all born of one mother. The ovaries of this group showed fully formed follicles, and in all of these ovaries some of the follicles were pluriovular.

The six ovaries of three animals about 3 months old were examined systematically, the sections chosen varying from about one-twentieth to about one-thirteenth of the total number. The pluriovular follicles found varied from 10 to 23 per ovary. Some of these were in the group of deeply placed, cord-like follicles; others were among the more peripheral, large follicles, and were often piriform or lobulated.

The relationship of these types to the pluriovular follicles of adult ovaries is raised by the article of Woerdeman (1921), who described a human ovary, probably adult, in which some of the pluriovular follicles had arisen, apparently, from medullary cords and were therefore homologous with seminiferous tubules.

Elongated follicles, each containing several ova in a row, mentioned by v. Schumacher and Schwarz, are apparently common in the opossum (Hartman,

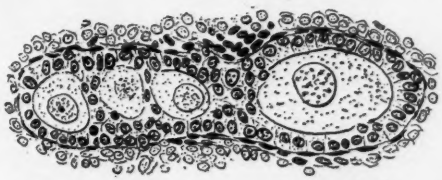


Fig. 3. One of the elongated cord-like pluriovular follicles, rarely found in the adult ferret. (× 410.)

1926). They occur, but are very uncommon, in the adult ferret (fig. 3). Those I have seen are small follicles, lying in the cortex, and do not differ, except in shape, from the other pluriovular follicles. In the adult ferret I have found no evidence that pluriovular follicles arise from medullary cords. V. Winiwarter and Sainmont considered it questionable whether the medullary structures in the adult cat were the same as those of the young animal.

The prevalence of degeneration in the pluriovular and other follicles in the young ferret ovary (as in that of the young cat, v. Winiwarter and Sainmont) indicates that we must account for the pluriovular follicles of the adult by factors present there, as has been attempted above. Nevertheless, the young ovary is of value in this study, because, as Kingsbury pointed out, it illustrates the effects of varying relationships of follicular tissue and stroma. The young ferret ovaries indicate that the lack of balance between these two groups, incident to growth and development, is responsible for the greater frequency of the pluriovular follicle, and also for the greater variety of shape. One of the most striking facts in the three-months' ovary is the comparative infrequency of pluriovular follicles among the small follicles closest to the periphery—

those which have been produced when the relation of connective tissue to follicular tissue resembles most closely that of the adult.

GROWTH AND DESTINY OF THE PLURIOVULAR FOLLICLE

(*a*) *Conversion to Uniovular Follicles* by the ingrowth of stroma—a view entertained, as regards small, especially primordial follicles, by a number of authors, some of whom, however, regarded other fates as also possible. It has been held by Quincke, Schottländer (1893), Hellin, Stöckel, Rabl, and Hansemann. In the adult ferret it does not appear to be at all common for even the smallest pluriovular follicles, as defined earlier in this paper, to be converted in this way. The process appears more probable in young ovaries, but there it is likely to be accompanied by degeneration.

(*b*) *Degeneration of the Contents.* Instances of this were described and discussed by Honoré and by Hansemann; and atresia was accepted as the common fate by Janosik, Schmaltz, and by Hartman (1926).

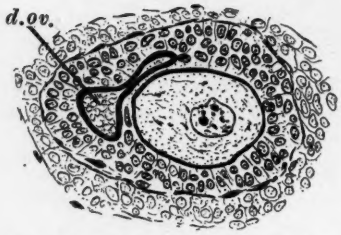



Fig. 4. A bi-ovular follicle. The ovum, *d.ov.*, with thicker zona pellucida, is much degenerated. (× 410.)

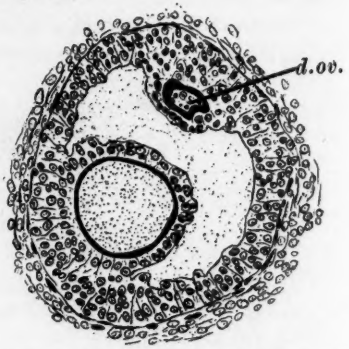



Fig. 5. A follicle showing ova in separate cumuli at opposite sides of the follicular cavity. One ovum, *d.ov.*, is much degenerated. (× 155.)

The evidence of degeneration in ovum, follicular epithelium, or both, noted during the examination of the 100 ferret pluriovular follicles, may be summarised as follows:

Follicles with no liquor folliculi (total: 46): 12 with signs of degeneration; 4 doubtful.

Follicles with a trace of liquor folliculi (total: 19): 11 with signs of degeneration; 4 doubtful.

Follicles with liquor folliculi in moderate or large quantities (total: 33): 31 with signs of degeneration.

From the remaining two follicles the liquor had apparently been absorbed in the process of degeneration.

Great differences in the degree of degeneration in different ova in the same follicle have been noted (figs. 4 and 5).

(*c*) *Growth.* (1) Growth of the ova. The ova in a pluriovular follicle may be all equally developed (Schrön, O'Donoghue, Arnold). Non-degenerate bi-ovular follicles may contain ova unequally developed (Loeb, 1901). Primordial ova may be contained in advanced follicles along with larger ova (Schottländer, 1893; Loeb, 1917; Hartman, 1926). It was as small ova that Statziewitch (see Alexenko) and also Schottländer (1893) interpreted the "Nährzellen" of Nagel. (Hartman, 1926, suggested that Schottländer, Nagel and others had before them different structures—true ova and swollen granulosa cells. The latter are common in or near the cavity of atretic follicles in the ferret (fig. 6), but the resemblance to ova is usually only superficial.)

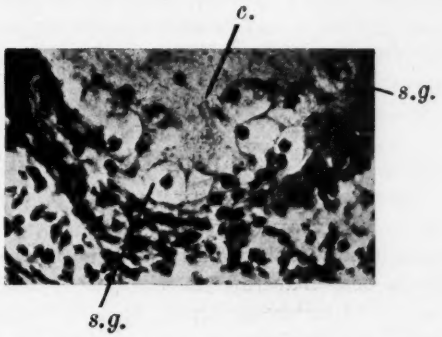



Fig. 6. Swollen granulosa cells, *s.g.*, near the cavity, *c.*, of a large atretic follicle. The nuclei stain more uniformly than do those of ova. (Fixed in Maximow; stained by Heidenhain's Iron-haematoxylin. × 400.)

In the examination of the 100 ferret pluriovular follicles, examples of the various types just mentioned were met. As revealed by the examination of serial sections, without actual measurement of ova, 37 out of the 100 follicles contained ova that were obviously different in size from their companions.

Attempts to account for this disparity are various:

(i) Inclusion of a small follicle in a larger one (Loeb, 1917). This theory has already been discussed, and has not been substantiated for the ferret.

(ii) Arrested development of the smaller of two ova in the same follicle (Arnold). This might account for some cases, but in some follicles the more developed ovum is the one showing obvious degeneration, the less developed being apparently healthy (fig. 4, p. 150).

(iii) Different thresholds of response to growth stimuli, whatever these may be (Hartman, 1926). This appears to be the most satisfactory explanation. Near pluriovular follicles, it is quite common to see ova which differ in size, and yet, from their position, may be presumed to have arisen at the same time, and now appear to be in a similar environment. The finest environmental differences escape histological demonstration, but it appears probable that

individuals differ in their capabilities even at this early stage of their life history. Similar considerations apply to the variation in extent of degeneration, noted above.

(2) Growth of the follicle, and maturation. Many of the pluriovular follicles described in the literature are small, even primordial (e.g. those of Stöckel, Rabl, Hansemann). Large follicles have, however, been recorded (e.g. those of Schulin, v. Franqué, Welch, Smyth, O'Donoghue).

The sizes of 100 ferret pluriovular follicles were estimated in cubic millimetres. They varied from 0·000,041 c.mm. to 0·74 c.mm. The smallest had one layer of cubical epithelium; the largest had many layers of polygonal epithelium and abundant liquor folliculi.

The following ripe pluriovular follicles are on record: one in a dog (Bischoff, 1845); two in *Dasyurus* (O'Donoghue); one in a pig (Corner, 1915).

I have not seen a mature pluriovular follicle in the ferret.

## THE RELATIONSHIP OF PLURIOVULAR FOLLICLES TO FERTILITY

"Fecundity" was the term used by Pearl "to designate the innate reproductive capacity of the individual organism, as denoted by its ability to form and separate from the body mature germ cells." It is with this, rather than with general fertility that we are concerned here. The relationship of pluriovular follicles to fecundity might be one of two chief types:

(*a*) *Co-existence with Diminished Fecundity* or sterility (Loeb, 1917). The evidence from ovulation rate in the ferret (mentioned below) inclines in this direction, but is quite inadequate.

(*b*) *Co-existence of the Follicles with Increased Fecundity.* This might imply either direct influence upon the fecundity, or an indirect relationship—the presence of a common cause.

(1) Direct influence upon the fecundity.

(i) Monochorionic twinning was held by Rosner and Ancel to be due to the liberation of more than one ovum from one follicle. This contention was criticised by Cuénot and, as regards the armadillo, with which species Rosner was concerned, it has not survived before the constructive work of Newman and Patterson on specific polyembryony (Newman and Patterson, 1910; Patterson, 1913; Newman, 1917).

(ii) Dichorionic twinning. V. Baer suggested that rupture of a pluriovular follicle would account for cases in which the (total) number of ova liberated was greater than that of the corpora lutea. Cases of this nature have been recorded (Bischoff, 1842; Corner, 1915; Lillie). In none of these, however, is it clear that monozygotic twinning or polyembryonic budding can be excluded. Adequate proof of the liberation of two ova from one follicle can emerge only from a complete examination of ova and ovaries soon after rupture of the follicles. Two animals in the series at present under consideration furnish useful

evidence in this respect. From each, both ovaries with oviducts were preserved as a complete series of sections, with the recently liberated ova still within.

Animal No. 1. Corpora lutea of the one ovary numbered 5; with 5 ova corresponding. Corpora lutea of the other ovary numbered 3; the ova numbered 4. Three of these were at the 7- or 8-cell stage of segmentation; the other was a well preserved unsegmented ovum of about one-third of the volume of each of the others; its nucleus was clearly defined, but showed no signs of maturation.

Both ovaries contained pluriovular follicles.

Animal No. 2. The left ovary contained 7 newly ruptured follicles; the ova corresponding numbered 7. The right ovary contained 3 newly ruptured follicles; the ova corresponding numbered 4. Of these, three were in the oviduct in the pronuclear stage; the fourth was in the periovarian space, was of similar size to the others, but was probably degenerating. No pluriovular follicles were seen in a thorough examination of both of these ovaries.

(2) Indirect relationship of fecundity and the pluriovular follicle. Hellin, v. Franqué and Hartman (1926) have held that the tendency to fertility, manifest in twinning or in large size of litter, conduces to the production of numerous ova and to the formation of pluriovular follicles.

Various points in this view call for discussion.

(i) Concomitance of numerous small follicles with pluriovular follicles. Even if this concomitance were accepted as a general rule, which is not supported by evidence from the adult ferret, it is not clear that a tendency to fertility is manifested by simple abundance of small follicles. It is equally possible that the latter merely indicates a retention to some degree of a non-mature condition by the ovary, and in the non-mature state pluriovular follicles are fairly frequent. Hellin, indeed, admitted this relationship between abundance of follicles, presence of pluriovular follicles and immaturity; but looked upon more fertile species (multiparous) as less highly evolved, as regards reproduction, than the less fertile (uniparous). The ovaries of the multiparous were more embryonic in structure. Against this, it may be urged that, within a species, the fertility of younger animals is, as a general rule, less than that of somewhat older ones (Marshall, 1922). It appears that this lower fertility is actually due to lower fecundity (Hammond). Unless, therefore, the term "tendency to fertility" be taken as synonymous with "abundance of oocytes," there appears to be, as the work of Pearl showed, little relationship of this abundance to fecundity. Some other evidence must, therefore, be sought, if it is desired to prove a relationship between pluriovular follicles and fecundity.

(ii) Ovulation rate. In the opossum, there is, undeniably, co-existence of the follicular abnormality with high ovulation rate, stated to be 22 per animal (Hartman, 1926; see also Hartman, 1919). For the dog, in which it seems probable that pluriovular follicles are frequent, statistics of the ovulation rate are not extensive. The averages from three small sets of figures, given by widely separated observers, have been calculated, and are as follows:

5·4 per animal (Bischoff, 1845: ova, corpora lutea or recently ruptured follicles from 11 animals); 5·2 (Bonnet, 1897: corpora lutea from 11 animals); about 6·4 (Marshall and Halnan, 1917: corpora lutea from 7 animals). On account of the variation in prenatal death in different species (Robinson, 1921; Corner, 1923), litter size is not a satisfactory substitute for ovulation rate; but it may be mentioned that Heape gave the average litter for large breeds of dogs as 7·5 (1464 litters), and for terriers as 5·4 (1158 litters). The dog cannot be looked upon as an extremely fertile animal, and it is improbable that the actual fecundity is very great.

On the other hand, species may be mentioned in which high fecundity is unaccompanied by frequency of the pluriovular follicle. The collection of pig ovaries concerning which we have the most definite pronouncement upon the rarity of pluriovular follicles, is that of Corner. The ovulation rate of these animals (Corner, 1923) suggests that they belong to breeds of rather under the average fertility of British animals, as indicated by Wallace, who held that a sow ought to rear 10 or more pigs in each litter after the first. In view of the size of the animal, however, the fecundity of the pigs studied by Corner is still to be looked upon as high, the lowest average ovulation rate being $8{\cdot}109 \pm {\cdot}118$ per animal (in a group of 156 sows).

Again, Hill gave data from ovulation rate which led him to consider that *Dasyurus viverrinus* had a great tendency to fertility. Yet, in this species, ovaries containing pluriovular follicles do not seem to be frequent in a series (O'Donoghue).

In the ferret, the number of ova shed at ovulation is 9·95 (Robinson, 1921); breeders consider the average birth rate per animal to be 6. Compared with the dog, the ferret has by no means a low fertility, and yet it does not show pluriovular follicles very frequently.

Individual instances of abnormally high fertility accompanied by pluriovular follicles in the ovary have seldom been reported, and the records are not convincing. Ten children had been borne by a woman of 41 whose ovary showed the follicular abnormality (v. Schumacher and Schwarz). Smyth's case of a fertile Gordon setter is sometimes quoted. The evidence has been criticised by Hartman (1926); the chief fault, as regards the present question, is that the ovaries of some of the offspring and not of the mother were examined. Woerdeman made an indirect reference to Strassman's case, in which it was alleged that the ovary of a woman who died while giving birth to twins was found to contain two ova in nearly every follicle. (I have been unable to consult the actual record.)

In the ferret series that has been examined, it has not always been possible to group the ovaries in pairs according to the animals to which they belonged; but the number of corpora lutea has been noted in the various ovaries. The average number of ova shed by each ferret ovary at one ovulation is just under 5. With this may be compared the following figures, obtained from the ovaries which showed the most abundant pluriovular follicles: Two ovaries

from one animal contained respectively 5 and 3 corpora lutea. Two from another contained respectively 4 and 3. Single ovaries, all from different animals, contained corpora lutea as follows: 4 (3 ovaries); 3 (2 ovaries); 1 (1 ovary).

It appears that the tendency to the production of pluriovular follicles may exist in the ovary of an animal which cannot be considered as very highly fecund.

Apart, therefore, from the rare possibility of two mature healthy ova being liberated from a follicle, there seems to be no necessary association of pluriovular follicles and increased fecundity.

## THE SIGNIFICANCE OF THE UNIOVULAR CONDITION OF FOLLICLES

The most obvious disadvantage of the pluriovular follicle, as a mode of reproduction, is exemplified by the instance given previously, in which, of two ova liberated from one follicle, one was by no means ready for liberation. The differences in growth rate between ova render the uniovular follicle a more suitable structure for ovulation than the pluriovular.

## THE IMPORTANCE OF THE PLURIOVULAR FOLLICLE IN RESEARCH

In the first place, the possibility of rupture of a pluriovular follicle has always to be borne in mind in the study of corpora lutea counts in regard to migration of ova, even in animals where the pluriovular follicle is no more frequent than it is in the ferret.

Secondly, if the chances of liberation of more than one ovum from a follicle are greater than in the ferret, statistics of prenatal death are apt to be affected, these being based on a comparison of the number of corpora lutea with the number of ova found at various stages of pregnancy.

## SUMMARY

Analysis has been made of the majority of the previous records of the pluriovular follicle in the ovaries of Mammals. This abnormality is widely distributed; but there has been great lack of standardisation in the accounts given, and there is little knowledge of the frequency of the condition in different species. The conclusions which appear justifiable are that the abnormality is frequently met in the opossum and dog; but is rare in *Dasyurus viverrinus*, in the Texas armadillo, in the pig (at least of some breeds), and probably in *homo*.

Four hundred and ninety-six complete ovaries of adult ferrets have been preserved as serial sections, and these have been surveyed. Certain groups of the ovaries, chosen at random, have been systematically examined. The con-

clusions drawn from them are: (1) pluriovular follicles occur with moderate frequency in the adult ferret, one or more being present in about one-third of the ovaries; and (2) the abnormal follicles are not abundant in any one ovary.

One hundred ferret pluriovular follicles have been investigated, and the data, in part numerical, form the basis of the subsequent discussion.

There appears to be no connection in the adult ferret between the presence of pluriovular follicles and (1) the presence of plurinucleated ova (of which no example was observed); (2) abnormal abundance of small follicles; (3) abnormal abundance of tubular ingrowths from the germinal epithelium.

The pluriovular condition does not appear to be due to secondary failure of the connective tissue intervening between follicles; but to the lack of balance in development between the follicular tissue and the connective tissue at the stage when the small follicles normally become separated from each other. Various conducing factors are suggested by specimens observed (p. 146).

In the 100 follicles examined, the bi-ovular type is the commonest; the greatest deviation from the uniovular being a follicle with at least 13 small ova.

The theory of origin of the zona pellucida is discussed in connection with the absence of the follicular epithelium between growing ova. The conclusion is, on the whole, in favour of the production of the zona by the ovum.

Thirty-nine ovaries of young (non-mature) ferrets have been examined. In this series ovaries containing pluriovular follicles were much more frequent than in adults; and the abnormal follicles in the individual ovaries were also more abundant. The conclusions with regard to the cause were confirmed by these specimens.

Differences in growth and degeneration between the ova of the same follicle are exemplified. The cause is apparently differences in the response of the various individual ova to the stimuli which promote growth or degeneration, as the case may be. Degeneration seems to be the usual fate of these follicles.

The relationship of the follicular abnormality to fertility, in particular to fecundity (Pearl), is treated. Two instances of the rupture of a pluriovular follicle are recorded in the ferret. Apart from the mere possibility of the liberation of two healthy mature ova from a follicle, there seems to be no necessary association of pluriovular follicles and increased fecundity in the ferret. The available data suggest that this conclusion is true of Mammals in general.

The most obvious disadvantage of the pluriovular follicle as a mode of reproduction, is exemplified by the liberation of a non-mature ovum.

The possible importance of the pluriovular follicle in research is mentioned (p. 155).

All the specimens used for the figures are from adult ferrets. Fig. 6 is from an untouched photograph. All the rest are from camera lucida drawings.

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While the above article was in the press there appeared a numerical study of the pluriovular follicle in the mouse by **E. T. Engle** (*Anat. Rec.* vol. XXXV, p. 341). Evidence is furnished that the condition is not frequently seen in the ovaries of this Rodent.

# A COMPARATIVE STUDY OF THE NICTITATING MEMBRANE OF BIRDS AND MAMMALS

By E. PHILIP STIBBE
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The necessity for a special mechanism to remove foreign bodies from the eye exists in all land animals, for the preservation of vision. This is not only on account of the immediate interference with vision that all foreign bodies must cause (either directly if situated on the cornea, or indirectly if not on the cornea), but the temporary interference with vision is likely to be followed by a permanent defect if the foreign body be lodged on the cornea. The cornea, like other parts of the body, has its own protective reaction, but this may go on to organisation; and unfortunately it is just in the case of a mechanical irritant that organisation is specially likely to occur. So that, failing the immediate and adequate removal of the foreign body by mechanical means, the result will be a permanent localised interference with vision. That is the reason for the extreme sensitiveness of the cornea; the intense pain caused by a foreign body is to be regarded as the measure of the urgency of the "S.O.S."

The nature of the protective apparatus may be expected to vary in different animals, according to their habitat; it will depend on the liability of the eyes to injury, and upon the needs of the animal in the matter of acuity of vision.

Crawling and burrowing animals—Amphibia, lizards, snakes—are specially liable to injury from dust and mud; but one may suppose that in most instances moderate clearness of vision would meet the necessities of the case.

Mammals, being mostly less near the ground, are correspondingly less exposed to dust and dirt; but one must remember grazing and browsing Mammals, forest life and winds.

Birds, one would say, are the least liable to eye-injury—that is flying birds; but even these are to some extent and at times exposed to dust. And if they are less likely than other animals to suffer injury to the eyes, the consequences of that injury when it does occur are much graver. For birds cannot afford to lose a fraction of their acuity of vision; they have to "spot" prey or enemies at long distances, and must be on the alert for obstacles when travelling at high speeds; so that the lesser frequency of the danger is counterbalanced by the greater acuteness of the danger.

It is to be noticed, also, that a bird cannot afford to have the eye covered, say by an opaque lid, even for a fraction of a second while in flight; that would be fatal while travelling at fifty or sixty miles an hour amongst tree-tops and branches.

The structure provided to meet this necessity for special protection of the eye is the well-known so-called "nictitating membrane"; and this is of interest

to human anatomists by reason of the association with it of the plica semilunaris of man. The customary definition of the human plica semilunaris is—"a vestige of the membrana nictitans or third eyelid, which occurs in Birds, Reptiles and Mammals, and is of use in cleaning the cornea" (1, 2).

Now, the implications of such a statement are twofold in nature—physiological and morphological.

Physiologically we state that there is in Birds, Reptiles and Mammals a membrane which nictitates—that is, moves rapidly to and fro over the front of the eye; and that the purpose of this nictitation is to cleanse the front of the cornea.

Morphologically we imply that this structure is the same thing in Birds, Reptiles and Mammals, and that ontogenetically or phylogenetically, or both, it is a third eyelid.

Finally we believe that this structure has lost its function in man, but persists as a vestigial structure, the plica semilunaris.

That is—it is hoped—a not unjust interpretation of the present view of the plica semilunaris and the nictitating membrane.

The purpose of this study is to confirm or modify our view of the nictitating membrane, by investigating the following points:

(1) What are the essential features—structural and functional—of a true nictitating membrane? For this purpose we study in detail the Bird, it being well established that the Bird has a true nictitating membrane.

(Exigencies of time have made it necessary to study only those types which might throw light on the Mammals; the Reptiles are regarded as highly specialised, and as no more likely to help than the Birds; on the other hand Amphibia have been introduced as being less specialised and therefore likely to throw light on the phylogeny of the membrane. The nictitating membrane of Reptiles has been investigated, and in general resembles that of Birds (3).)

(2) Have Mammals a nictitating membrane in the same sense—structurally and functionally—as Birds?

(3) What do we know of the comparative morphology of the membrane in Birds and Mammals?

(4) Is the plica semilunaris of man a vestigial structure, representing this membrane of Birds and Mammals?

## (1) THE NICTITATING MEMBRANE OF BIRDS, AND ITS NEURO-MUSCULAR MECHANISM

The nictitating membrane of Birds has been frequently and well described (4). It is found for example as far back as Owen (5). There can be no doubt that Birds possess a true physiological nictitating membrane, with a definite and highly-specialised neuro-muscular mechanism.

The membrane (fig. 1) is a triangular reduplication of the conjunctiva in the region of the inner or anterior canthus; it is almost invisible when not in

action, but covers a large part of the front of the eye when it is pulled outwards by its muscles. The apex of the triangle is at the inner canthus; the base—deeply concave—extends in a vertical direction across the front of the eye, from the junction of the inner with the middle thirds of the upper lid, to a corresponding point on the lower lid.

This edge of the membrane is usually everted and deeply pigmented, and its palpebral surface is raised into rough irregular ridges; the ridges are composed of heaped-up keratinised epithelium, and would appear to act as a sort of comb for the deep surface of the lids. The upper and lower edges of the triangular membrane merge into the conjunctiva at the fornices; the membrane has thus fornices deep and superficial to it.

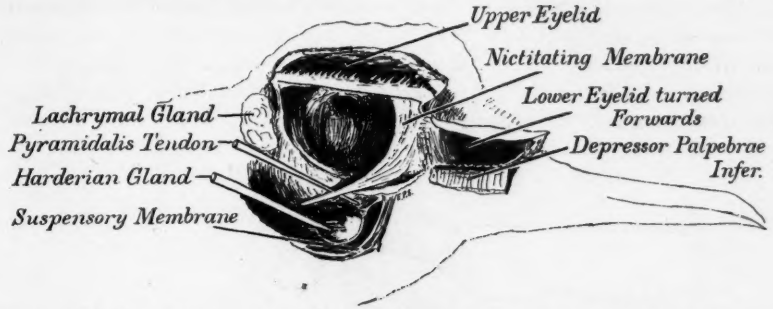


Fig. 1. Nictitating membrane of the Bird (ostrich) as dissected from the front. The lower eyelid has been turned forwards, and the pyramidalis tendon is seen extending round towards the back of the eyeball. Note also conjunctival fornices superficial and deep to the membrane.

The Bird sweeps the membrane across the eye with great rapidity and at frequent intervals without closing the eyelids; the membrane is semi-transparent so that vision is not greatly interfered with. One would suppose from cursory observation of Birds that the movement of the membrane was so rapid as not to permit of analysis in the living animal; but it appears to have been analysed by naturalists (4), who describe it as a pendulum-like movement, the membrane swinging across the eye from an upper fixed point; its rapidity under varying conditions has also been estimated.

By dissection the following points can be seen:

The upper angle of the membrane is firmly fixed into the upper conjunctival fornix; this fornix is shallow, and the upper lid is a short thick rigid structure, and appears not to be movable apart from the eyeball. This agrees with the observation that the upper angle of the membrane does not move. The lower angle blends also with the fornix of the conjunctiva, but this latter is loosely attached to the lid and globe; and the fornix is deep, and the lower lid freely and independently movable.

*The pyramidalis muscle.* Attached to the lower angle of the membrane is a strong flattened tendon, the tendon of the pyramidalis muscle (fig. 1). This

is seen to be coming forwards round the outer side of the eyeball to its insertion into the membrane. The pyramidalis (fig. 2) arises from the outer surface of the sclerotic at the inner side of the eyeball; it is a thin conical slip of muscle, with its free end directed backwards and outwards towards the optic nerve. Before reaching the optic nerve, it ends in a tendon, which has already been seen at the front of the eye; so that this tendon has to wind round the back and outer side of the globe, forming nearly three-fourths of a circle, to its insertion. The pyramidalis thus encircles three sides of the eyeball, lying in close contact with the sclerotic, and pulling, as it were, right round the eye; an arrangement which evidently assures that the membrane will remain in contact with the cornea as it is pulled round.

The manner of insertion of the pyramidalis tendon reminds one of the insertions of the chordae tendineae of the valves of the heart; the tendon spreads out in the substance of the membrane, so that tendon and membrane are a continuous sheet; the effect of this is to prevent any tendency to puckering of the membrane as it slides across the eye.

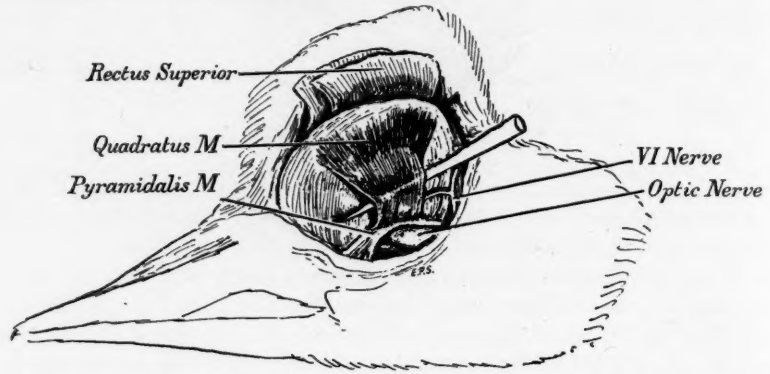


Fig. 2. Orbit of ostrich dissected from behind, to show pyramidalis and quadratus muscles, and their nerve supply from the sixth cranial nerve.

*The quadratus muscle.* The action of the pyramidalis is modified and reinforced by that of a second muscle, the quadratus (fig. 2). This arises from the sclerotic immediately behind the insertion of the superior rectus; its fibres are directed backwards as a broad flat sheet under cover of the superior rectus, and in contact with the sclerotic. It is inserted into a narrow fibrous pulley-like tunnel placed transversely above the optic nerve; this fibrous sheath invests the tendon of the pyramidalis, which it holds up off the optic nerve; in the specimen shown the pulley-form is not perfect, the quadratus appearing to gain partial insertion actually into the tendon of the pyramidalis. According to Owen (5) and other observers, the action of the quadratus is to prevent the tendon of the pyramidalis from pressing on and injuring the optic nerve.

The quadratus would appear however to have another function; the writer suggests that it is a tractor of the membrane of no less importance than the pyramidalis; the two muscles act together, to fix the direction of pull of the pyramidalis tendon in one direction, no matter what be the position of the eye. This is represented in fig. 3.

Looking at the back of the eye, let $Q$ represent the pull and the line of action of the quadratus; $Q$ can be resolved into two parts at right angles—$Q'$ along the tendon, and $Q''$ at right angles to it. If $\alpha$ be the angle between $Q$ and $Q''$, then $Q''=Q\cos\alpha$. Similarly $P$ can be resolved into $P'$ along the tendon, and $P''$ at right angles to it; and $P''=P\cos\beta$. In a position of equilibrium, the downward pull of the pyramidalis is equal to the upward pull of the quadratus; that is, $Q\cos\alpha=P\cos\beta$.

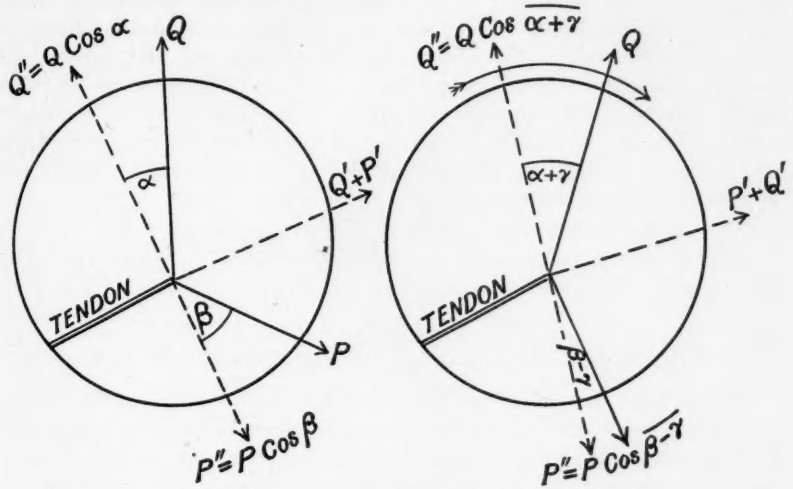


Fig. 3. Diagram to represent action of pyramidalis and quadratus, as explained in text.

Now let the eye be rotated inwards through an angle $\gamma$. The angle $\alpha$ now becomes $\alpha+\gamma$, and the angle $\beta$ becomes $\beta-\gamma$, that is to say that as the eye rotates inwards $\cos\alpha$ diminishes, and therefore $Q\cos\alpha$, the upward pull of the quadratus, diminishes by an amount proportionate to the angle of rotation of the eye; and $P\cos\beta$, the downward pull of the pyramidalis, is similarly increased. The tendon will therefore move downwards till the angle of rotation $\gamma$ is abolished—that is, the tendon will return to the position of equilibrium.

Similarly if the eye be rotated outwards, the tendon will move relatively upwards till the angle of rotation is abolished.

This means that, whatever position the eye assumes, the tendon of the pyramidalis will move relatively to the globe, so that it always occupies the

same position in space; that is, the tendon will not move with the eye, but will always pull the membrane in exactly the same direction.

Such a constant direction of pull, whatever the position of the eye, could not be obtained by the action of one muscle; it can only be produced by two muscles like these, whose actions can be resolved into components in opposite directions.

The nerve supply of the pyramidalis and of the quadratus is from the sixth cranial nerve, which supplies the external rectus, and then turns inwards and backwards under the quadratus to end in the pyramidalis (fig. 2).

*The depressor palpebrae inferioris.* This muscle is also of interest in connection with the nictitating membrane. It is shown on fig. 1, where it has been detached from the broad suspensory ligament in turning the eyelid forwards. It is a part of the same sheet as this hammock-like suspensory ligament; and it passes forwards as a broad thin sheet to be inserted into the substance of the lower lid, and into the areolar tissue between the lower lid and the palpebral conjunctiva. When the nictitating membrane slides outwards, this muscle will fix the lid and prevent it from being also pulled outwards; in addition, by its conjunctival insertion, it will prevent the membrane from falling into horizontal folds, that is it will help to keep the membrane uniformly applied to the front of the eye.

The nerve supply of this muscle is from the third nerve.

Such is a sketchy account of the nictitating membrane of Birds. How does this compare with that of Mammals?

### (2) THE SO-CALLED NICTITATING MEMBRANE OF MAMMALS

Superficially this resembles the nictitating membrane of Birds. It is a crescentic reduplication of the conjunctiva in the inner angle of the orbit, projecting towards the cornea, of the same shape as in the Bird, with the concave free border, and a similar thick pigmented line adjacent to this border. Is this a nictitating membrane functionally?

It is usually described as sweeping over the front of the eye as the eyelids are closed, and possibly it does slide outwards to a certain extent; but it would seem not to be capable of sweeping out very far or easily; for it is a thick rigid structure with a stout cartilaginous basis, and the cartilage is attached into the subconjunctival tissues at the inner aspect of the eyeball, and also to the internal tarsal ligament.

Observation of living animals suggests that what is described as a movement outwards of the membrane might well be a rolling inwards of the eye under the membrane. But without insisting that this is the case, there is another reason for saying that the membrane of the Mammal does not truly nictitate—that is, does not move rapidly across the eyeball independently of the lids—namely that it has not got the necessary muscular apparatus for independent movement. The writer has made numbers of dissections of the

orbits of calves, sheep, rabbits and cats, all of which have a well-marked "nictitating membrane," and has failed to find any specialised apparatus for moving the membrane. The examination of serial sections across the fold has revealed at the most a few scattered bundles of unstriped muscle fibres. The nearest approach to a muscle of the nictitating membrane is the levator palpebrae superioris (fig. 4). This muscle (say in the calf) has a wide expansion to its conjunctival insertion—closely resembling the expansion of the human muscle. The inner part of this insertion may be traced as a fairly definite band into the substance of the membrane; it may slightly protrude the membrane, and probably tenses it and helps to fix it while the eyeball rolls inwards under it.

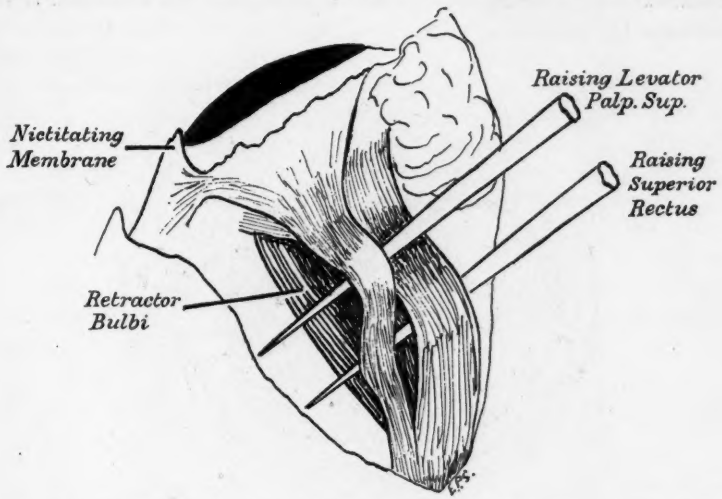


Fig. 4. Superficial dissection of orbit of calf from above, to show connection of levator palpebrae superioris with membrane. Note that the deep muscle—the retractor bulbi—has no connection with the membrane.

In addition, the smaller Mammals, notably the cat, have a poorly developed sheet of retractor fibres, with an indefinite origin in the subconjunctival tissue superficial to the internal rectus. Note that these fibres, like the levator palpebrae, are in the superficial or subperiosteal plane.

There appears to be no muscle directly moving the membrane—nothing to suggest functionally a pyramidalis or quadratus.

Structurally the nictitating membrane of Birds is a simple membranous structure containing a goodly proportion of elastic tissue (fig. 6), but that of Mammals is a complex structure. In fact the essential element in the mammalian plica is not membrane, but a cartilage which has evaginated the conjunctiva. This cartilage is no mere nodule, but a large plate of elaborate design, and most exactly fitting its special purpose of picking up particles from

the front of the eye. For reasons that will be given, it is proposed to call this the INTERCEPTING CARTILAGE, and the membrane the INTERCEPTING MEMBRANE—CARTILAGO ET MEMBRANA INTERCIPIENS LACHRYMARUM, terms which more correctly indicate the nature of their function.

It is also formally proposed to drop the term "nictitating membrane" when speaking of Mammals.

*The intercepting cartilage.* This is shaped something like a pickaxe, with a stout, rather flattened handle and a long thin blade. It is quite a large structure, being in the calf more than half an inch long, and in a small Mammal like the rabbit more than a quarter of an inch long; while the thin blade stretches vertically across the cornea, and is of the same length as the maximum vertical diameter of the cornea.

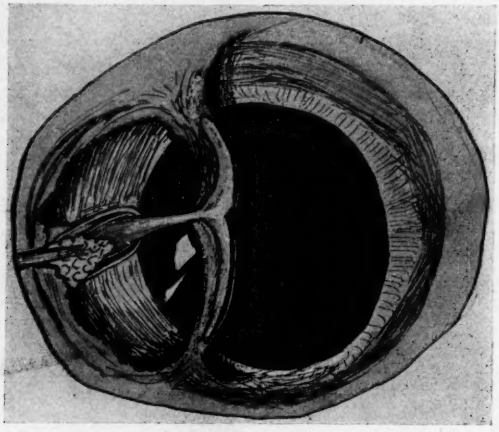

Fig. 5. Dissection to show the structure of the nictitating or intercepting membrane of a calf.

The handle or horizontal limb of the cartilage is stout and somewhat club-shaped, its thicker end being buried in the subconjunctival tissue at the inner side of the eyeball, under cover of the structures at the inner canthus. To its superficial aspect is attached a deep membranous prolongation of the internal tarsal ligament. The cartilage extends outwards, curving round the inner side of the globe, and becomes slender as it approaches the cornea. Near the inner margin of the cornea it joins the blade or vertical limb which occupies the margin of the evaginated conjunctiva—that is to say, the main limb splits into two limbs at right angles to its long axis.

The cartilage thus forms a sort of "squeegee" at the inner side of the orbit, under which the eyeball can roll. The cartilage is of course covered on both sides by conjunctiva, so that there is a deep internal fornix between it and the

globe, and a shallower superficial internal fornix between it and the lids. The part of the internal fornix bounded by the lower lid is the lacus lachrymalis, and is open internally, where it becomes flush with the skin at the side of the root of the nose; at the junction of skin and conjunctiva is the caruncula lachrymalis.

The blade or vertical limb of the cartilage extends exactly across the greatest width of the cornea, and is curved to lie accurately on the convexity of the globe. The corneal aspect is smooth; the palpebral aspect of the conjunctival covering is raised into a series of thick irregular ridges, pectinate in appearance and palpable to the finger.

*The Harderian gland* (fig. 5). In Birds this gland is situated at the back of the orbit, and drains into the deep internal fornix; there is also a lachrymal gland draining into the outer part of the upper fornix.

In Mammals the Harderian gland is situated in the substance of the nictitating membrane. It covers the superficial aspect of the inner two-thirds of the handle of the cartilage, and is to some extent wrapped round on to its deep surface. The gland has from one to four ducts; these are most easily demonstrated in the calf, in which there are four; they open at the bottom of a small pouch on the ocular surface of the membrane, at a point a short distance within the free edge of the membrane. The ducts wind across the borders of the cartilage to pierce the conjunctiva; they are sufficiently large in the calf to take bristles, and can then be dissected out; their length outside the gland is about half an inch.

The secretion of the gland is thick and sticky. These Mammals have the usual lachrymal gland at the upper and outer part of the orbit, with a serous secretion.

## MICROSCOPIC APPEARANCES IN BIRD AND MAMMAL

(Figs. 6, 7 and 8.)

*In the Bird* the nictitating membrane has a basis of fibrous tissue, most of the bundles tending to be longitudinal, but some crossing these at right angles (fig. 6).

The membrane is said to retract by its own elasticity, and one confidently looked to find much elastic tissue in it. In picro-carmine sections, however, while the elastic tissue is very evident, it cannot be said to be excessive.

The conjunctival covering consists of stratified epithelium which, on the palpebral surface, is strongly heaped up, especially near the free edge of the membrane where it forms the pectinate ridge already alluded to. There is no glandular tissue in the membrane; the duct of the Harderian gland opens into the deep internal fornix.

*In the Mammal* the following are the microscopic appearances (fig. 7):

The cartilage is hyaline with very plentiful cells which appear to be rather small, and which exhibit no very definite grouping.

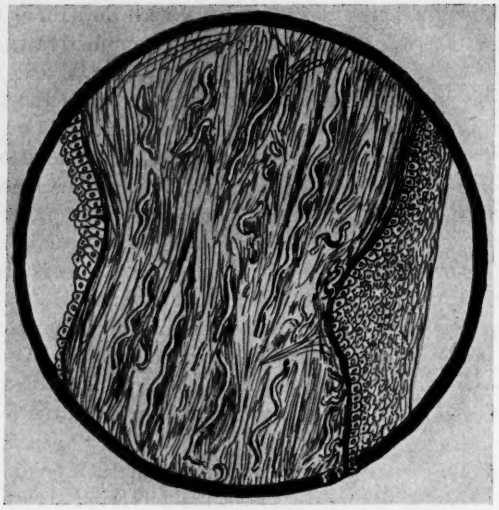

Fig. 6. Section across the nictitating membrane of a cock stained with picro-carmine to show yellow elastic tissue.

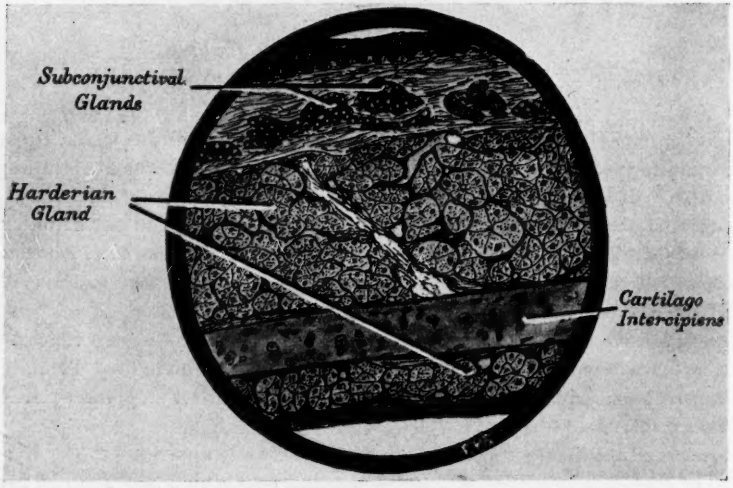


Fig. 7. Cross section of the nictitating membrane of a calf.

The Harderian gland is in its greater part a typical alveolar serous gland, and would pass for a serous salivary gland. There is however a peculiar part of the gland near its inner or anterior end (fig. 8). It consists of round or oval alveoli lined by cubical epithelium, and containing a homogeneous colloidal-looking substance; some alveoli contain cell debris which has been desquamated from the alveolar wall, and give the impression that the cells are undergoing a colloidal change. Moreover, the interalveolar spaces are largely filled with cuboidal epithelial cells with large round nuclei, and interstitial substance proper is scanty. The writer is not certain of the interpretation of this appearance; it would almost pass for an adenomatous goitre. The substance of the membrane, other than gland and cartilage, is made up of compact areolar tissue.

Fig. 8. Section of the colloidal portion of the Harderian gland of a calf.

The membrane is lined on its palpebral surface by a stratified epithelium, set on small papillae; and on its ocular aspect by a single or double layer of rather flattened cells.

## THE FUNCTION OF THE PLICA OF MAMMALS

The physiological explanation of the plica and cartilage of Mammals is to be found in the consideration of the manner in which the eye gets rid of foreign bodies; and the human eye furnishes a satisfactory means of investigating this. If one goes out in a dust storm, one's eyes rapidly fill with dust, and as rapidly get rid of it. Where does the dust go? It will be found collected together into a little sticky mass at the inner canthus; and that mass is situated on skin, in

the angle internal to the caruncula lachrymalis, in which situation it causes no irritation and does no damage. There can be no doubt that this is brought about by the intervention of the plica semilunaris, which is not so vestigial a structure as the descriptions of it might imply; it is in fact a very respectable fold, with an underlying conjunctival fornix often a quarter of an inch in depth.

When a foreign body gets on to the eyeball, two mechanisms are set working. First there is an excessive secretion of tears, the object of which is to float the object up off the surface of the globe. The lids are instinctively closed, thus forming a sort of cistern, so that the front of the eye is freely bathed, and a light object will be floated forwards.

It is probably a reasonable conjecture that the photophobia of foreign bodies is a purposeful reflex; the temptation to close the eye persists in the dark.

The hypersecretion of tears is accompanied by the well-known action of the orbicularis palpebrarum, which sweeps tears and foreign matter across to the inner side of the eye, and *past* the openings of the lachrymal canaliculi—not into the canaliculi. It must be remembered

(*a*) that the orifices of the canaliculi are very minute—about one-tenth of a millimetre in diameter;

(*b*) that the flood of tears has raised the orifices from contact with the eyeball;

(*c*) that the orifices tend to face down-stream, especially when the orbicularis is in action.

It is therefore reasonable to suppose that foreign particles cannot escape by the lachrymal canaliculi.

Now the internal conjunctival fornix is bridged across by the plica semilunaris, which in man has a very thin free concave edge, like the lunula of a watch-pocket valve of the heart. So the tears and foreign matter are diverted forwards across the caruncular region. The caruncle is closely packed with large glands resembling sebaceous glands (fig. 9). The foreign body thus reaches a region of fine hairs and much fatty sebaceous material, and the rest of the story is obvious.

If the eye be kept open when there is a foreign body in it, the ball will be seen to be repeatedly turned inwards, in an effort to get the body picked up by the plica and diverted towards the caruncular region. An eyelash, for example, has been observed in a patient's eye; it was carried inwards by the tears and the action of the orbicularis, but slipped *under* the plica semilunaris; it was brought out from this position by an outward sweep of the eye abolishing the deep internal fornix; and after several trials it was finally picked up by the plica, and transferred to the skin at the inner canthus.

It is for these reasons that the terms PLICA INTERCIPIENS and CARTILAGO INTERCIPIENS have been suggested.

Incidentally it would seem that the correct treatment for a foreign body in the eye is to close the lids and wait.

Such would appear to be the mechanism in man and Mammals, and it fits in well with our conception of their requirements; Birds must have the speediest method possible, Mammals can sacrifice speed in this matter to thoroughness.

Fig. 9. Section across human caruncula lachrymalis, showing numbers of large glands closely packed together.

## WHAT DO WE KNOW OF THE MORPHOLOGY OF THE NICTITATING MEMBRANE, AND OF THE INTERCEPTING MEMBRANE AND CARTILAGE?

The writer has not yet been able to make the attempt to trace the ontogeny of the mammalian membrane and cartilage; it would therefore not be proper to form any definite views as to its morphological value, though it may not be out of place to express a very tentative opinion that the mammalian structures are morphologically different from those of the Bird, an opinion based on the belief that the neuro-muscular mechanism constitutes a morphological entity, as suggested below.

The same uncertainty is not felt, however, in regard to the nictitating membrane of the Bird; it can definitely be homologised with a part of the lower eyelid of certain of the Amphibia, as exemplified by the frog and the newt.

The following considerations are suggestive:

*The eyelids of the frog* (fig. 10). The upper lid of the frog resembles that of the bird, being short and somewhat rigid with a shallow conjunctival fornix; and it moves up and down with the eye, and appears unable to move

independently of the eye. The lower lid is wide with a deep fornix, and moves freely and independently of the eye; and it is transparent in its upper two-thirds. The eye is closed by drawing the lower lid up over the lower three-fourths of the globe, and at the same time turning down the eye itself which carries with it the upper lid, and so the lids meet. This lower eyelid resembles a nictitating membrane in its transparency, and in addition it bears comparison with the nictitating membrane in respect of (1) its position; (2) its muscular and nervous mechanism.

(1) When the lower lid is not in use, the transparent upper part slides down within the opaque lower part; that is, it comes to occupy the plane between the ocular conjunctiva and the palpebral; this is the position of the nictitating membrane of the Bird. We can thus differentiate the lower lid of

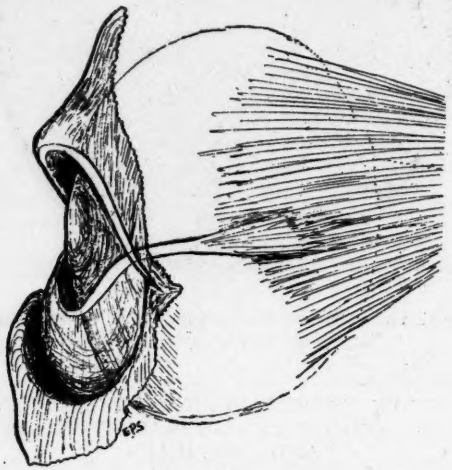

Fig. 10. Diagram of eyelids of frog, with pyramidalis muscle seen from outer side.

the frog into two parts—the inner transparent nictitating part, and the outer opaque skin-covered lid-part. Now a vertical section across this compound lower lid has the same appearance as a section across the developing lids and nictitating membrane of a chick (3) (fig. 11). Ontogenetically the lower lid is a double or bifurcating outgrowth.

In the anurous Amphibia the inner part of this double lid grows more rapidly and to a greater size than the external; this results in the differentiation of the adult lid into its two parts as described. In the Bird the two parts of the developing lid grow more equally, resulting in a separate nictitating membrane under cover of a well-marked and freely movable lower lid (3).

The study of developing chicks earlier than the eleventh day suggests that the nictitating or inner part may be the primary lid, and the part which becomes the lower lid a secondary outgrowth from the nictitating membrane.

The nictitating membrane of the Bird is of course at the internal canthus, but this need not cause great difficulty in comparing it with that of the frog. The upper lid of the frog always overlaps the lower at the external canthus; if we slightly rotate the lower lid of the frog so that the outer angle becomes the lower, and the inner angle slips up under the upper lid, we have the position of the nictitating membrane of the Bird. And, as we shall see, the outer angle of the lid of the frog has the pyramidalis muscle attached to it, thus corresponding with the lower angle of the true nictitating membrane. Such a change in position would be brought about by a change in the direction of the rima palpebrarum, namely a relative descent of the anterior or inner end of that fissure. Tentatively it may not be fantastic to suppose that such a change might be associated with the development of a frontal region of the brain, and of a roof to the orbit.

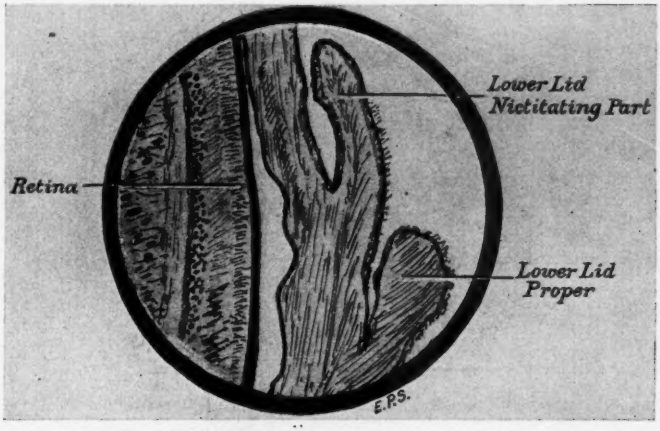


Fig. 11. Vertical section of developing lower eyelid and nictitating membrane of chick—10 days.

(2) *The neuro-muscular apparatus.* The lower eyelid of the frog is elevated by a tendon inserted into its outer angle. This tendon pierces the conjunctiva of the upper lid, just above the external canthus; it then runs back through the fibres of the pterygoid muscle (which, in the frog, occupies the outer part of the orbit), and is continued back to a muscular belly arising from the outer side of the sclerotic. But this muscle is not an isolated entity; it is a partially detached portion of the choanal or retractor bulbi muscle. The choanal muscle wraps round the optic nerve, is intimately related to the external rectus, and is supplied by the sixth nerve.

The elevator of the lower lid of the frog thus can be compared to the muscles of the nictitating membrane of the Bird; these are part of a deep sheet

around the optic nerve and posterior part of the eyeball, are closely related to the external rectus, and are supplied by the sixth nerve.

Now, if the eye muscles are the representatives of three pre-otic head segments (6), the immediate pre-otic being supplied by the sixth nerve, and the most anterior segment by the third nerve, then we may reasonably say that the pyramidalis of the Bird is morphologically the same as the elevator of the lower lid of the frog; it is proposed to call this latter muscle the pyramidalis of the frog.

The frog has also a depressor palpebrae inferioris, which is part of a complete muscular sling, and corresponds to the fibrous sling and depressor muscle of the Bird (fig. 1). This muscle is in both cases supplied by the third nerve, and therefore belongs to the first segment of the head.

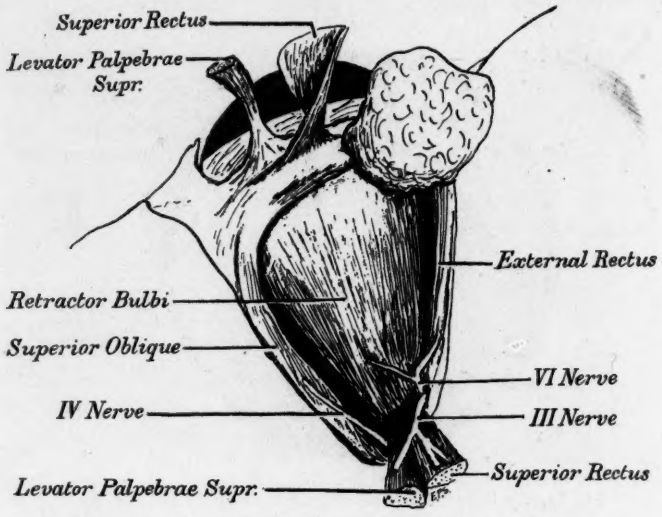


Fig. 12. Retractor bulbi muscle of calf, dissected from above.

*Neuro-muscular apparatus in the Mammal.* We have seen that structurally and functionally the plica of the Mammal differs from that of the Bird, and that its neuro-muscular mechanism—if any—is also different from that of the Bird. We now have to face the fact that the Mammal has nevertheless a well-marked retractor bulbi muscle, corresponding to the choanal muscle of the frog and to the two muscles of the nictitating membrane of the Bird, yet this muscle shows no anatomical connection with or relation to the plica.

The retractor bulbi is present in all the Mammals dissected for this investigation as a well-marked thick muscular cone, folded round the outer side of the optic nerve and almost completely surrounding it; it is inserted into the sclerotic behind the recti, under cover of which it lies (fig. 12). There are

described in Mammals protrusor fibres (represented in man by the sphenoidal-fissure-fibres of Müller), and it is supposed that these push the eye up to the plica, and the retractor bulbi pulls it back again. Without entering into the merits of this view, we may simply say it does not make these muscles anatomically the mechanism of the plica. Further, the retractor bulbi is closely related to the external rectus, and is supplied by the sixth nerve.

One is tempted therefore to think there are two distinct mechanisms—a third-nerve mechanism for eyelid, and a sixth-nerve mechanism for nictitating membrane.

In the frog both mechanisms are present in connection with the lower lid; in the Bird both are present in connection with two separate structures—lower lid and nictitating membrane; in the Mammal both are present, but the sixth-nerve mechanism has no connection with plica or lid.

In conclusion, it has been assumed that the plica semilunaris of man is the same as the plica of Mammals; cartilage has been found in the plica of negroes, and occasionally in Europeans. The writer has as yet not found any cartilage in a number of sections of the plica semilunaris.

## SUMMARY

(1) A special protective apparatus for the eye is necessary in all land animals, and will vary according to habitat and needs.

(2) It is generally stated that the plica semilunaris of man and the nictitating membrane of Mammals, Birds and Reptiles are representatives of the same structure; this is our problem.

(3) The following steps towards the investigation of the problem are taken, in order:

(*a*) Full investigation of a typical nictitating membrane and its neuromuscular mechanism, as seen in a Bird—the ostrich.

(*b*) Comparison of this with the so-called nictitating membrane of Mammals, and discussion of the function of the mammalian structure and of the plica semilunaris of man.

(*c*) Estimation of the probable morphological value of the nictitating membrane of the Bird, by comparison with the lower lid of the frog, and by study of its ontogeny.

(4) These studies lead to the following conclusions:

(*a*) That structurally and functionally the plica of man and Mammals differs entirely from the nictitating membrane of Birds. It is proposed to drop the term "nictitating membrane" in speaking of Mammals, and to call the plica the "plica intercipiens" and its cartilage the "cartilago intercipiens."

(*b*) That there is reasonable ground for supposing that the plica of man and Mammals is morphologically different from the nictitating membrane. But the morphology of the mammalian structures has yet to be worked out by a study of their ontogeny before any definite conclusion can properly be stated.

Acknowledgment has to be made to Professor W. H. Wood for permission to do this work in the Anatomy Department of Liverpool University, and for the advantage of many discussions of the subject with him; to Dr J. Beattie, of the Zoological Gardens, for material; and to Professor Sir Arthur Keith for that interest and advice which he is always so ready to give.

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# CONGENITAL DISPLACEMENT OF THE SHOULDER JOINT

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E.W., a male, aet. 46, was admitted into one of the Medical Wards of King's College Hospital under Dr A. C. D. Firth on 13 July of last year, suffering from myelogenous leukaemia. During routine examination by the Medical Clerk it was noticed that both shoulders were of abnormal appearance, though the patient did not complain about them. He (the patient) said that the shoulders had been like it since birth, and that they had never troubled him.

The patient had been told that he was a premature child, and that there had been a difficult labour—to use his own expression, a "strangled birth." He came of a poor stock. The mother died at an early age, and the father, still living, suffers from "an incurable nervous disease." Of six brothers and sisters, only one healthy brother survives. The patient himself is a widower, and childless. Both testes had remained undescended.

One was removed in 1920, and no trace of the second could be found at the post-mortem examination. He was of the eunuch type, with hairless face, feminine type of figure, and long lank limbs.

Both shoulder joints were abnormal. The acromion process, on either side, was unduly prominent, and the normal prominence of the deltoid muscle was absent. A prominence formed by the dislocated head of the humerus could be felt posteriorly on both sides. There was no paralysis of muscles, and function was surprisingly good, there being comparatively little limitation of movements.

X-rays (fig. 1) showed a bilateral posterior subluxation of the joint, with very marked malformation of the acromion and coracoid processes, and a misshapen humeral head.

A diagnosis of bilateral congenital subluxation was made. On 30 September the patient succumbed to the malady for which he was admitted, and the specimen described below was obtained at the autopsy. The specimen is now in the Museum of the Royal College of Surgeons.

*Description of Specimen.* Viewed from behind, the outstanding deviations from the normal are immediately appreciated in the shape of the scapula body, the tortuous spine, the irregular acromion, and the articular facet on the posterior aspect of the scapula neck (*C*, fig. 2).

There is no trace of a glenoid cavity in the normal situation.

Attention is directed to the articular facet. It is not glenoid in shape, but its surface is divided into an upper convex portion and a lower concave portion.

The upper portion, which is the larger of the two, is formed entirely by the base of the coracoid, and the lower portion by the neck of the scapula.

The facet is invested on its posterior margin by a tough fibrous ligament representing the true glenoid ligament. The gleno-humeral capsule is complete. The biceps tendon (long head) arises, as in the normal, from the supraglenoid tubercle, and can be seen emerging from the bicipital groove of the humerus (fig. 3). The origin of the long head of the triceps from the infraglenoid tubercle, and the insertions of the teres minor, infraspinatus and supraspinatus into the greater tuberosity of the humerus are all normal.

The articular surface of the humerus is misshapen to some extent. It is broader and flatter than normal, and only the lower and inner surface appears to come into contact with the scapula facet. The rest of the head is covered with cartilage, which shows pittings, probably the result of rheumatoid arthritis.

The coracoid process points directly outwards instead of outwards and forwards as in the normal. Instead of consisting of a short vertical limb and a longer horizontal limb, its direction is horizontal from the first.

The spine of the scapula is so rotated that the normally superior surface faces forwards, and the normally inferior, backwards. The twist is carried upwards into the acromion, which exhibits a very marked degree of malformation. It is so rotated that it lies horizontally with an upper and a lower surface, instead of, as in the normal, postero-superior and antero-inferior surfaces. The acromio-clavicular joint is normal in situation. The small irregularities normally present on the external border of the acromion to which fasciculi of the deltoid are attached, have become exaggerated to form three well-defined prominences.

The body of the scapula appears flatter than normal. Its vertebral border is practically straight. The superior angle is far less acute than normal, and the superior border is horizontal, and directly continuous over the suprascapular notch (which in this case is a foramen) with the superior border of the horizontally disposed coracoid process.

## DISCUSSION

There are two possible explanations of the condition:

1. The head of the humerus subluxated from the glenoid cavity, either during intra-uterine life or within the first few weeks of infancy, and a new articular facet formed on the posterior aspect of the neck of the scapula, with complete disappearance of the original glenoid.

2. The articular facet present is the original glenoid cavity in an unusual position, and not an adventitious one formed as the result of posterior subluxation of the humerus.

From the examination of the specimen there can be little doubt that explanation 2 is the correct one. As already described, the biceps tendon (long head) arises from the upper margin of the existing glenoid (*c*, fig. 2), i.e. it bears

a normal relation to the glenoid, and by this identifies the latter as the true facet. If this glenoid were adventitious, the biceps tendon would have arisen from the axillary border of the scapula at a point corresponding to the supra-glenoid tubercle of the normally placed articular facet. This anatomical point proves, I think, beyond dispute, that the existing glenoid is the original cavity appearing in an unusual position.

Reference to the description of the specimen shows that the coracoid process itself points directly outwards instead of outwards with an inclination forwards. The process appears to have been rotated backwards during an early stage of development, with the result that the articular portion of the base faces backwards and outwards instead of directly outwards. The head of the humerus has been carried backwards with the articular surface, and an ectopic joint has resulted. The lower and minor portion of the glenoid has not shared in the rotation, at any rate to the same degree. This portion is developed from the scapula body and has no separate epiphysis, so that one could not expect rotation to occur apart from the scapula itself. The triceps origin has retained its normal relation with the axillary border of the scapula. The joint has, in fact, never subluxated, but has been carried bodily backwards. Subluxation is retained as a descriptive term, however, for reasons of simplicity.

The anomalous position of the joint has affected the trend of development of the other bony elements, and there has resulted the deviation from normal of the scapula body and its acromion process, and the head of the humerus.

## LITERATURE

The literature of congenital subluxation, though comparatively small, is very controversial. There is no unanimity of opinion as to the etiology of the condition, and as to its relation with subluxation secondary to birth palsy. The two conditions are hopelessly confused, and it seems very probable that a large number of so-called congenital subluxations, if not the majority of the published cases, are instances of the latter condition in which the paralysis has recovered. The possibility of traumatic dislocation occurring at birth must, also, not be overlooked.

Smith, early in the nineteenth century, wrote extensively upon congenital subluxation, but recognised no distinction between paralytic subluxation and the true congenital type. For him, all subluxations dating from birth were entitled to be called congenital, and a great number of cases he describes so carefully are undoubtedly of paralytic origin. The post-mortem appearance of one case, however, bears a very striking resemblance to the present case. The deformity, according to the engravings accompanying Smith's publication, is identical, except for a slightly different appearance of the humeral head. The case was that of a woman aged 40 who had a bilateral subacromial subluxation. No history of the case, which was not seen by Smith before death, was recorded.

In 1866 Loignan wrote a thesis for the Paris doctorate on the subject of congenital luxation of the shoulder. It contains little of value beyond a des-

cription of experiments he made upon the foetus with a view to determining the possibility of traumatic dislocation during birth. He found that he could not dislocate the shoulder by manipulation. The constant lesion which occurred if sufficient force were used, was a fracture of the humeral shaft through the soft bone underneath the epiphysis.

Duchenne, Vallorbe and others had previously obtained the same result. Loignan concluded on these grounds that subluxation of the shoulder in infancy is never traumatic.

Stimson attempted to clarify the subject by classifying congenital subluxation in the following way.

Group I. Cases due to irregular development of the joint.

Group II. Cases in which the bones are normally formed, and in which the displacement may have occurred during delivery.

Group III. Cases in which the bones are normal, in which displacement is the late result of a paralysis, antedating birth or caused during delivery.

Royal Whitman at a later date adopted practically the same classification.

The classification is, however, open to criticism. It is obvious that the cases comprising Group III differ entirely in their etiology from the others suggested, and can scarcely be regarded as congenital subluxations. They are definitely paralytic subluxations, no less so than paralytic dislocations of the hip joint secondary to anterior poliomyelitis. A better descriptive term to apply to these cases would be paralytic subluxation of the new-born.

Group II admits of the possibility of traumatic subluxation, though this has been strongly discredited by the French School. Taylor, writing in 1921, also refutes the possibility. It is his belief that there is no such thing as congenital subluxation of this joint. He bases this conclusion upon the fact that neither he nor any of three obstetricians attending large lying-in hospitals had ever seen a case of Erbs palsy in which the subluxation preceded the paralysis. T. T. Thomas, writing in 1914, is, on the other hand, firmly of the opinion that traumatic dislocation not only occurs, but is the primary factor with regard to the paralysis. His thesis is that obstetrical palsy is secondary to subluxation occurring as the result of trauma during delivery. The evidence he puts forward is not, however, convincing, and his theory is not generally favoured. Fairbank, in the previous year, had clearly shown that the subluxation is secondary to paralysis.

The possibility of traumatic dislocation finds another supporter in Phelps. He based his views upon the operation findings in three cases of supposed congenital subluxation. The first case was in a boy of 8, who had had a posterior subluxation of the shoulder since infancy. At operation, Phelps found "with the aid of my finger that the posterior border of the glenoid had been broken away, and that the cavity was about two-thirds its normal size." In the other two cases the findings were the same.

It is difficult to place any reliance upon this observation. To be able to palpate at operation an eight-year-old fracture which had, presumably, occurred

at birth, is more than can be expected, and it seems more probable that these were cases either of paralytic subluxation of the new-born, or of congenital subluxation, in which the posterior border of the glenoid was defective in a way similar to the acetabular margin in congenital dislocation of the hip joint.

With regard to Group I, Stimson regards Smith's case as the only recorded example of subluxation due to irregular development of the joint. The majority of authors who favour the possibility of congenital subluxation also regard this case of Smith's as the only one recorded. I cannot think this to be true, for there are cases in the literature which appear to be of undoubted congenital origin, and yet which do not present the gross deformity of Smith's case and of the case described above. I think it probable that the view-point of the authors referred to has arisen from a misinterpretation of the facts. I believe Smith's case and the present case to be examples of a very rare condition brought about by intra-uterine forces in which the coracoid process, as described above, has been bodily rotated backwards, with resulting subluxation, or ectopia of the joint as a whole. As such, these cases must constitute one type of intra-uterine subluxation. The other cases which appear to me to be of intra-uterine origin, i.e. congenital, probably differ entirely in the mechanism of their displacement. In them, the glenoid, though possibly poorly developed, remains in its original position, and the condition found is exactly analogous to congenital dislocation of the hip joint, the further migration of the axial bone in the latter condition depending upon the anatomical features peculiar to the hip joint. In this group should be placed the cases comprising Group II of Stimson's classification, the theory of their being cases of traumatic dislocation being discarded.

The following four cases are, I think, examples of this type of congenital subluxation.

Two of the four cases are described by Scudder, and occurred in a brother and sister, aged 9 and 7 respectively. Both had a posterior subluxation of the right humerus, noticed soon after birth. The clinical picture in both was identical. There was no paralysis, and X-rays showed little deformity beyond a general smallness of the bones of the affected side.

A third case is recorded by Frosch. The patient was a girl aged 10 years, with a bilateral posterior subluxation of the humerus noticed soon after birth. There had never been any paralysis of muscles, and function had remained almost perfect. An X-ray photograph showed a "rudimentary" coracoid process and glenoid cavity, but the humeral head was normal. The biceps and deltoid muscles were intact, and there was no muscular abnormality.

The fourth, and unpublished case, is one seen by Mr H. A. T. Fairbank at the Hospital for Sick Children, and I am indebted to him for permission to mention it here.

The patient, a boy, was seen when 3 years old, and had a posterior subluxation of the right shoulder joint. There was definite limitation of movement at the joint, but no paralysis of the deltoid. The condition was associated with a

congenital deformity of both hands ("claw-hands") and bilateral talipes equino-varus.

## SUMMARY

1. A case of bilateral posterior displacement of the shoulder joint is recorded, together with a description of the appearances found at post-mortem examination. The displacement is thought to be due to bodily rotation backwards of the coracoid process during intra-uterine life. This is an extremely rare condition, only one case of a similar nature having been recorded previously.

2. Subluxation of the shoulder joint associated with birth palsy should be excluded from the category "congenital."

3. The trend of evidence, both clinical and experimental, is opposed to the possibility of traumatic dislocation occurring during delivery.

4. Congenital subluxation of the shoulder joint, comparable with congenital dislocation of the hip joint, and differing in its mechanism of production from the case described in the text, does occur.

I wish to thank Sir Arthur Keith for his kindness in having the specimen dissected at the Royal College of Surgeons, and for permission to use the accompanying illustrations.

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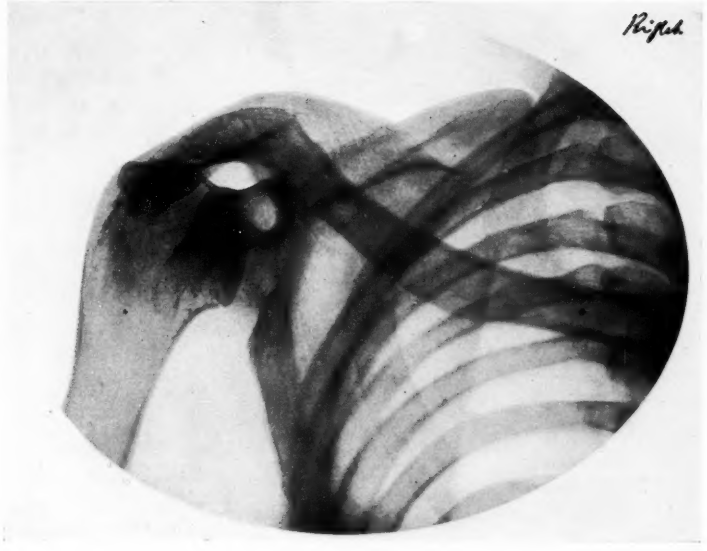
## DESCRIPTION OF PLATES

Fig. 1. Skiagram showing the deformity of the shoulder joints. It will be noticed that there is little difference in appearance of the two sides.

Fig. 2. The right shoulder joint from behind. For description, see text.

Fig. 3. The humeral head from in front. Note the well-formed capsule of the joint, and the origin of the long head of the triceps.



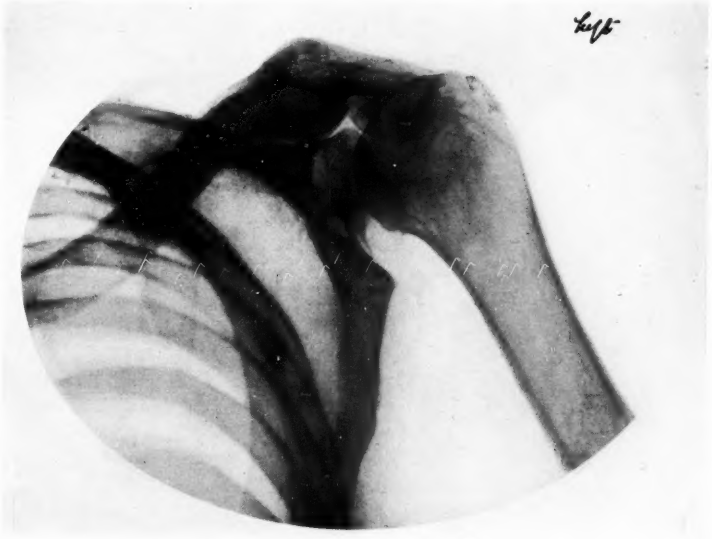




Fig. 1.

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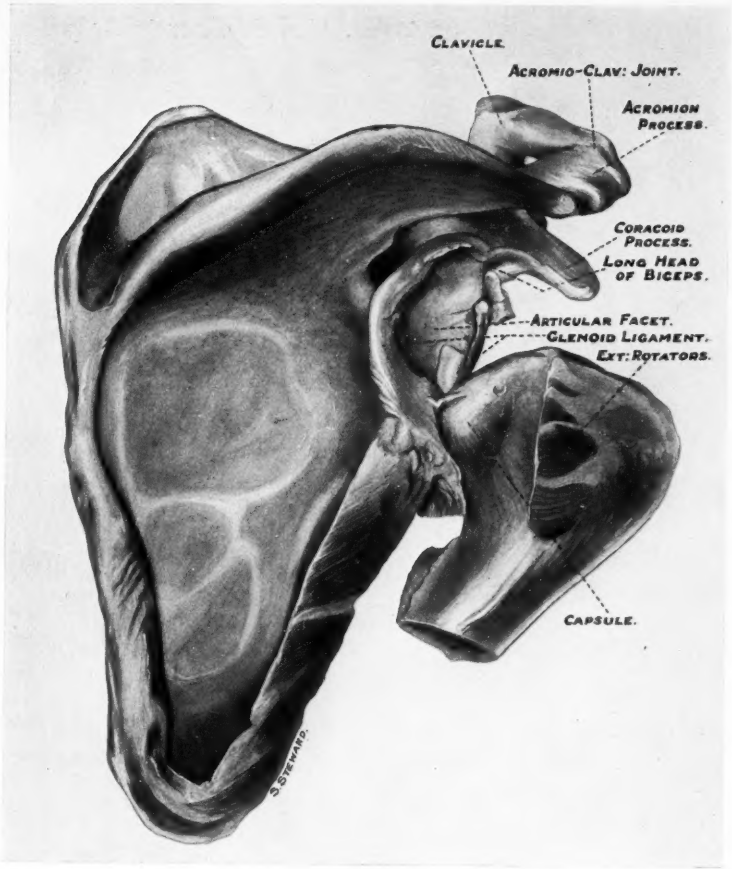
CLAVICLE.
ACROMIO-CLAV: JOINT.
ACROMION PROCESS.
CORACOID PROCESS.
LONG HEAD OF BICEPS.
ARTICULAR FACET.
GLENOID LIGAMENT.
EXT: ROTATORS.
CAPSULE.
J. STEWART.

Fig. 2.

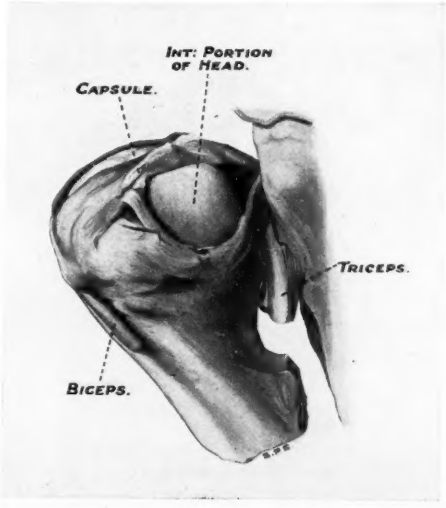
INT: PORTION OF HEAD.
CAPSULE.
TRICEPS.
BICEPS.

Fig. 3.

COLWELL—Case showing Abnormal Epiphyses of Metatarsals and First Metacarpals

# CASE SHOWING ABNORMAL EPIPHYSES OF METATARSALS AND FIRST METACARPALS

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The following case is of interest from its rarity. The subject was a boy aged four years, who was examined in the X-ray Department of King's College Hospital for a suspected injury to the ankle. No evidence of injury was found; but skiagrams of both feet show the unusual condition of proximal epiphyses to the metatarsals (II to V) with no trace of the usual distal epiphyses.

The first metatarsal of the left foot shows in addition a suggestion of a distal epiphysis, but this does not occur on the right side.

Both hands show a well-marked distal epiphysis for the metacarpal bone of the thumb which, indeed, is much better developed than the co-existing normal proximal epiphysis.

No morphological importance seems to attach to these unusual epiphyses which, indeed, are regarded as false or pseudo-epiphyses. The question of abnormal epiphyses of the metacarpals and metatarsals has been epitomised in a paper by Wakeley[1] in the *Journal of Anatomy* for July 1924.

[1] Wakeley, C. P. G. "Bilateral epiphysis at the basal end of the second metacarpal." *Journ. Anat.* vol. LVIII, pt. 4, p. 340, 1924.

# FOUR CASES OF ANOMALOUS INFERIOR VENA CAVA WITH AN EXPLANATION OF THEIR DEVELOPMENTAL ORIGIN

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## INTRODUCTION

During the past few years four cases of anomalous inferior vena cava have been observed in the dissecting room of this department. At the suggestion of Prof. Gowland, we have assembled the particulars of these cases and here present them with a brief discussion of their probable developmental origin. The developmental interpretation is in each case based on the recent work of McClure and Butler[1]; to illustrate our remarks we have prepared, from the figures given by these writers, the composite diagram which constitutes our fig. 1.

To Dr J. Mark, Dr M. A. Radcliffe-Taylor, and Mr C. J. C. Britton we are indebted for particulars in connection with certain of the cases.

A bibliography of the anomalies of the inferior vena cava is appended.

## I. CASE OF LEFT INFERIOR VENA CAVA (Fig. 2)

### *Description of case*

The subject was an adult male (Italian).

The inferior vena cava in this case may be divided into three parts according to its relation to the aorta.

(*a*) The first part, corresponding to the postrenal portion of the vessel, lay on the left side of the aorta, which it displaced to the right of its normal position. The vena cava was formed at the level of the fourth lumbar vertebra, below and a little to the left of the bifurcation of the aorta, by the union of the two common iliac veins, and ascended on the left side of the aorta to the level of the first lumbar vertebra, where it received the left renal vein. The left spermatic vein, instead of entering the left renal vein, joined the inferior vena cava about $1\frac{1}{2}$ inches below the entry of the left renal vein.

(*b*) The second part of the vena cava lay ventral to the aorta, passing obliquely upwards and to the right. It received on its left aspect the left suprarenal vein.

[1] McClure, C. F. W. and Butler, E. G. "The Development of the Vena Cava Inferiorin Man." *Amer. Journ. Anat.* vol. xxxv, p. 331, July, 1925.

(*c*) The third part of the vessel lay to the right of the aorta, and received the following tributaries, in order from below up:

(1) A large vessel which, for reasons to be explained later, we may term the persistent right supracardinal. This vessel itself was joined, about ½ inch below its union with the inferior vena cava, by the right spermatic vein, and below this again by a large lumbar vein which appeared to be the chief tributary of the persistent right supracardinal, causing a sudden increase in its size.

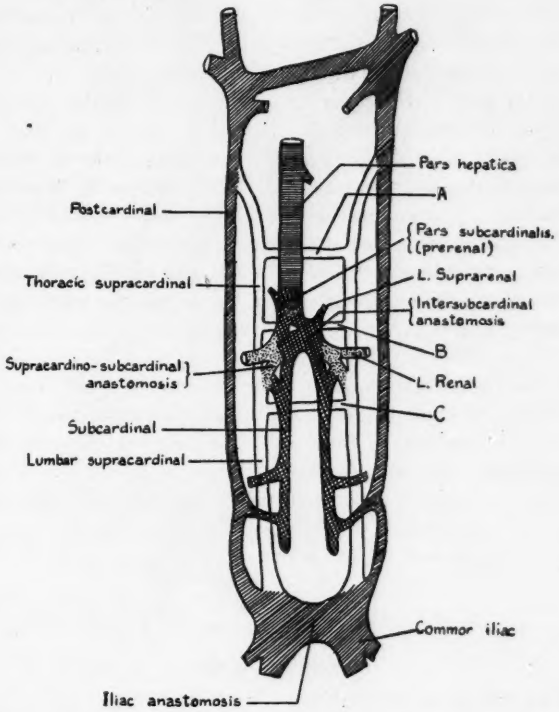


Fig. 1. Composite diagram to show the development of the human inferior vena cava. Prepared from a series of figures given by McClure and Butler.
*A*, *B*, and *C* = Intersupracardinal anastomoses.

(2) The right renal vein, which entered the inferior vena cava just above the persistent right supracardinal and almost together with it, though the two could hardly be said to form a common trunk.

(3) The right suprarenal vein, which entered the inferior vena cava about ½ inch above the entry of the right renal vein. Above the entry of the right suprarenal vein the course of the inferior vena cava was normal.

### *Developmental Interpretation*

According to McClure and Butler, the postrenal part of the inferior vena cava consists of the right lumbar supracardinal vein together with part of the supracardino-subcardinal anastomosis (fig. 1). We believe that in this case the postrenal vena cava is a reversal of the normal and therefore consists of (1) the left lumbar supracardinal, into which drain the two common iliac veins, and (2) the left supracardino-subcardinal anastomosis, joined by the left renal vein. As already stated, the left spermatic vein joined the inferior vena cava, not the left renal vein; this is in agreement with the abnormal development and is what is usually found in cases of left inferior vena cava.

The prerenal part of the vena cava consists of (1) the intersubcardinal anastomosis, (2) the pars subcardinalis (prerenal), and (3) the pars hepatica.

The large vessel which joins the inferior vena cava on the right we have called the persistent right supracardinal. According to McClure and Butler, the right lumbar supracardinal has the following characters: (1) above, it joins the inferior vena cava just at the entry of the right renal vein; (2) it receives the right spermatic vein; and (3) below, it joins the right common iliac vein. The vessel which we have termed the persistent right supracardinal (1) opened above into the inferior vena cava just below the entry of the right renal vein, (2) received the right spermatic vein, and (3) was probably connected with the right common iliac vein; certainly a small vein (fig. 2) was observed joining the right common iliac, and, although, owing to the small size of the veins in question at this level, the connection between this and the right supracardinal was not established by dissection, their direction and calibre seemed to indicate their continuity. We therefore believe that the vessel which we have termed the persistent right supracardinal may justifiably be regarded as a secondary right inferior vena cava.

## II. CASE OF DOUBLE INFERIOR VENA CAVA (Fig. 3)

### *Description of case*

The subject was an adult female.

The inferior vena cava was symmetrically double in its postrenal portion, the two vessels running up one on either side of the aorta and uniting ventral to it at the level of the entry of the left renal vein. The unusual feature of this case was the relatively oblique course of the two caval trunks. (Cases with such an inclination of the vessels have frequently but erroneously been ascribed to abnormally high union of the two common iliac veins.) Just above the union of the external and internal iliac veins on each side, the two symmetrical trunks were connected by a small transverse trunk which lay dorsal to the common iliac arteries and ventral to the body of the fifth lumbar vertebra.

The lumbar veins were more or less normal, and in any case did not affect the anomaly. The transverse lumbar veins from both sides joined the right

caval trunk in the usual way. Each ilio-lumbar vein joined the common iliac vein of its own side. The continuity of the ascending lumbar veins with the azygos veins was not demonstrated and is not shown in the figure.

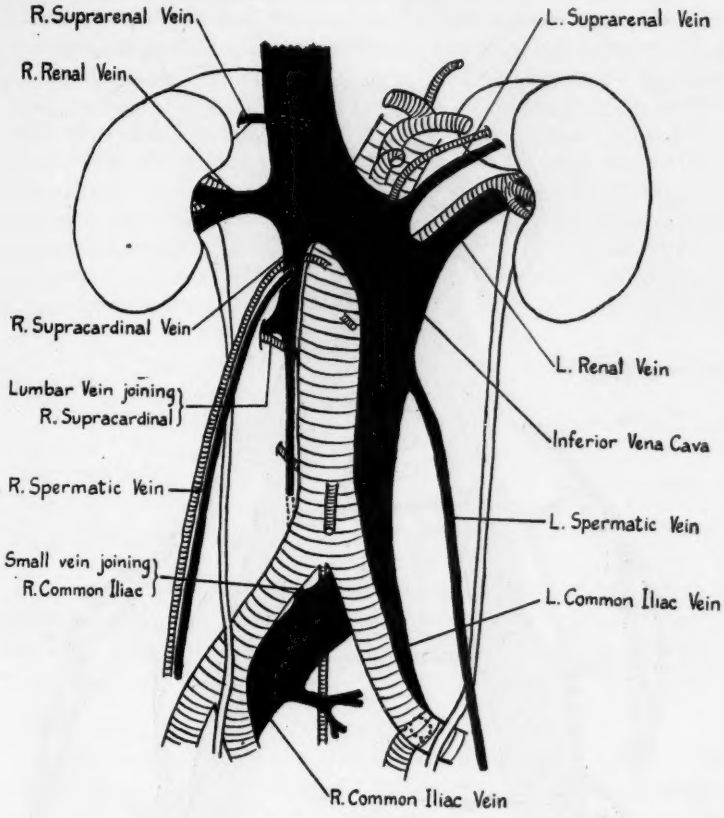


Fig. 2. The principal veins in Case 1 (Case of left inferior vena cava).

The right ovarian vein joined the right caval trunk at the normal level, while the left ovarian vein joined the left caval trunk at a corresponding level. A small vein, apparently lumbar, joined the right caval trunk a short distance below the entry of the right renal vein, and a similar one joined the left renal vein itself.

### *Developmental Interpretation*

McClure and Butler have shown that, in the early stages of development, the human inferior vena cava is symmetrical postrenally, consisting on each side of the following parts from below up: (1) the lumbar supracardinal,

connected below with the corresponding common iliac vein, which is united with its fellow by the iliac anastomosis, and (2) the supracardino-subcardinal

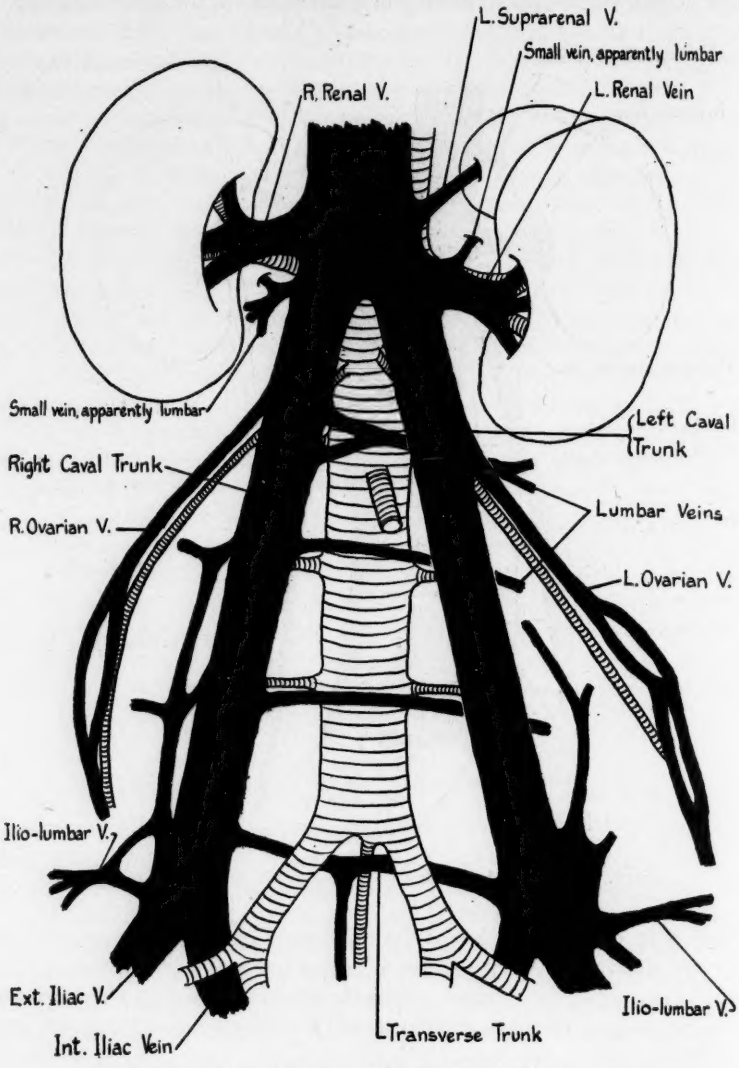


Fig. 3. The principal veins in Case 2 (Case of double inferior vena cava).

anastomosis. Above the level of the kidney the vessel is single, and consists of (1) the pars subcardinalis (prerenal) and (2) the pars hepatica.

The anomaly described above is by no means an uncommon one, and is due to persistence of both lumbar supracardinals instead of, as is usual, the right one only. Thus the inferior vena cava is double postrenally, and the right trunk consists of the same embryological parts as the normal postrenal inferior vena cava. The left trunk is the counterpart of the right and consists of corresponding parts, with the addition of the intersubcardinal anastomosis, which normally forms part of the left renal vein. The left renal vein is consequently shorter than usual, being only approximately as long as the right renal vein.

The transverse trunk mentioned in the description above represents a persistence of the embryonic condition in which there is a great iliac anastomosis in the same position. For this reason the position of junction of the transverse vessel with the caval trunks marks on each side the point of merging of the common iliac vein with the supracardinal vein. The right caval trunk, as we have already seen, represents the normal postrenal inferior vena cava, and the transverse trunk normally becomes incorporated in the left common iliac vein.

## III. CASE OF ANOMALOUS VENA AZYGOS MAJOR AND INFERIOR VENA CAVA (Fig. 4)

### *Description of case*

The subject was an adult male.

The chief characteristic of this case was the continuity of the vena azygos major with the inferior vena cava by two separate channels, which we may term the right and left communicating trunks.

The right communicating trunk arose from the right aspect of the inferior vena cava about ½ inch below the entry of the right renal vein; it then ran upwards and to the right, passing dorsal to the right renal vessels and dorsal to the medial part of the right suprarenal gland. It then inclined a little to the left, and, at the level of the dorsal attachment of the diaphragm, it united with the left trunk to form the vena azygos major.

The left communicating trunk arose from the left aspect of the inferior vena cava about 1 inch below the level of the entry of the renal veins (i.e., about ½ inch below the origin of the right trunk), and ran upwards and to the left to lie dorsal to the aorta and associated structures. It then arched to the right, dorsal to the main inferior vena cava, and finally, just after passing between the crura of the diaphragm, united with the right trunk to form the vena azygos major as above described.

The vena azygos major was much larger than usual, being about ⅝ inch in diameter. This enlarged vessel followed its normal course, receiving the usual segmental tributaries, and arching over the root of the lung to join the superior vena cava in the normal manner.

The prerenal part of the inferior vena cava had connected with it a small collateral vessel, which received the right suprarenal vein. This collateral vessel pursued an arched course, being connected with the inferior vena cava

(*a*) below, about ¾ inch above the entry of the right renal vein, and (*b*) above, just below the caval opening of the diaphragm. There were also present on the right side two small accessory renal veins.

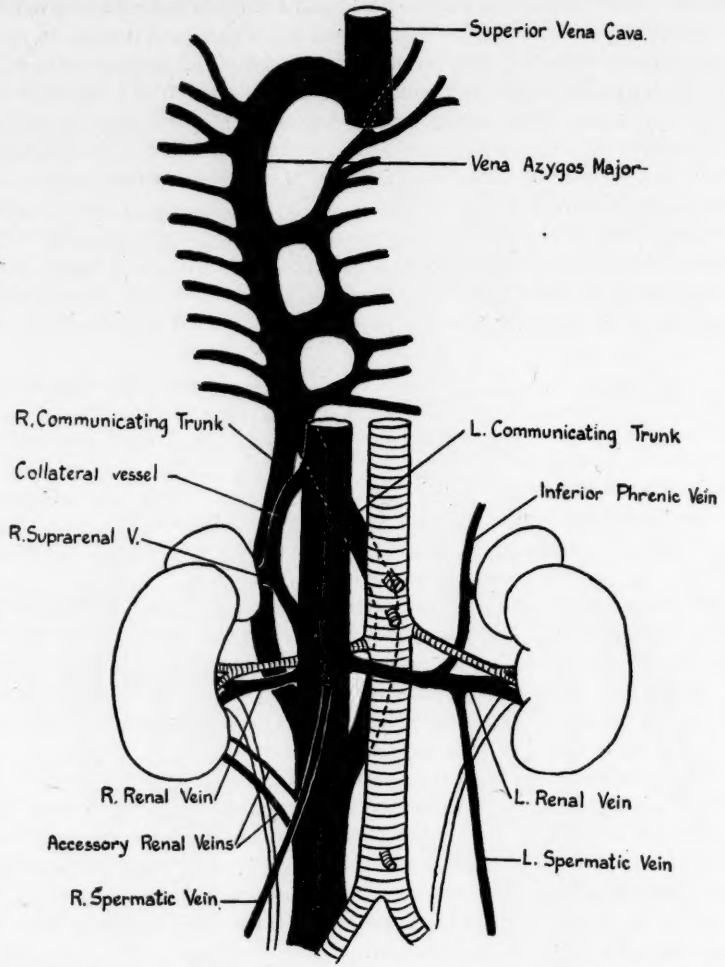


Fig. 4. The principal veins in Case 3 (Case of anomalous vena azygos major and inferior vena cava).

### *Developmental Interpretation*

In the early stages of the development of the inferior vena cava (fig. 1), the supracardinals continue from the lumbar region into the thorax, and unite above with the postcardinals on each side. There are also present several inter-supracardinal anastomoses (*A*, *B* and *C* in fig. 1).

In the present case, apart from the presence of the two communicating trunks, the postrenal inferior vena cava is normal and is formed in the manner already described. The right communicating trunk may be explained as being a persistence of the union between the thoracic and lumbar supracardinals on the right side. The left trunk is best explained as a persistence of (1) an intersupracardinal vein (*C* in fig. 1) in the lumbar region, below the renal vessels, (2) an intersupracardinal vein (*B* in fig. 1) just below the diaphragm, and (3) the part of the left supracardinal vein between these two intersupracardinals. This explanation accounts for the position of the left trunk dorsal to the aorta in part of its course, as well as its junction with the vena azygos major.

The small arched vein communicating with the prerenal part of the inferior vena cava is probably due to the enlargement of one of the capillaries from which the pars hepatica is formed. It may, however, be due to the enlargement of a capillary between the right suprarenal vein and the pars hepatica.

## IV. CASE OF OBSTRUCTED HEPATIC PORTION OF INFERIOR VENA CAVA (Fig. 5)

### *Description of case*

The subject was an adult female.

The part of the inferior vena cava between the entry of the right renal vein and the entry of the hepatic veins was represented by a fibrous cord 7 cm. long and 7 mm. in diameter. The cord was flattened, apparently by pressure of the viscera lying on it, but microscopic examination revealed its venous structure. The hepatic veins and the part of the inferior vena cava between them and the right auricle were normal, as was also the postrenal portion of the inferior vena cava.

From the upper extremity of the postrenal inferior vena cava the blood passed by two large channels, which we may term right and left.

(*a*) *The Right Channel.* This arose from the dorsal aspect of the inferior vena cava at the level of the entry of the right renal vein. It ascended vertically and passed through the aortic orifice of the diaphragm to continue as the vena azygos major, which opened into the superior vena cava in the usual manner. At the level of the first lumbar, eleventh, tenth, and ninth thoracic vertebrae, the vena azygos major was connected by four transverse anastomoses with the vena azygos minor; it received the right intercostal veins, the spinal branches of the tenth and eleventh being enlarged.

(*b*) *The Left Channel.* Arising from the inferior vena cava opposite the entry of the right renal vein, this channel first coursed transversely to the left, passing ventral to the aorta; it then turned downwards, but almost immediately doubled back on itself in order to proceed vertically upwards, lying on the bodies of the vertebrae to the left of the aorta. It pierced the diaphragm at the level of the second lumbar vertebra, and thereafter continued as the vena azygos minor, which in its lower part was slightly tortuous. The vena azygos

minor in its turn was continuous with the left superior intercostal vein, which opened above into the left innominate vein.

The abdominal part of the left channel received the following tributaries: (1) about the middle of its transverse part, the right ovarian vein; (2) at the

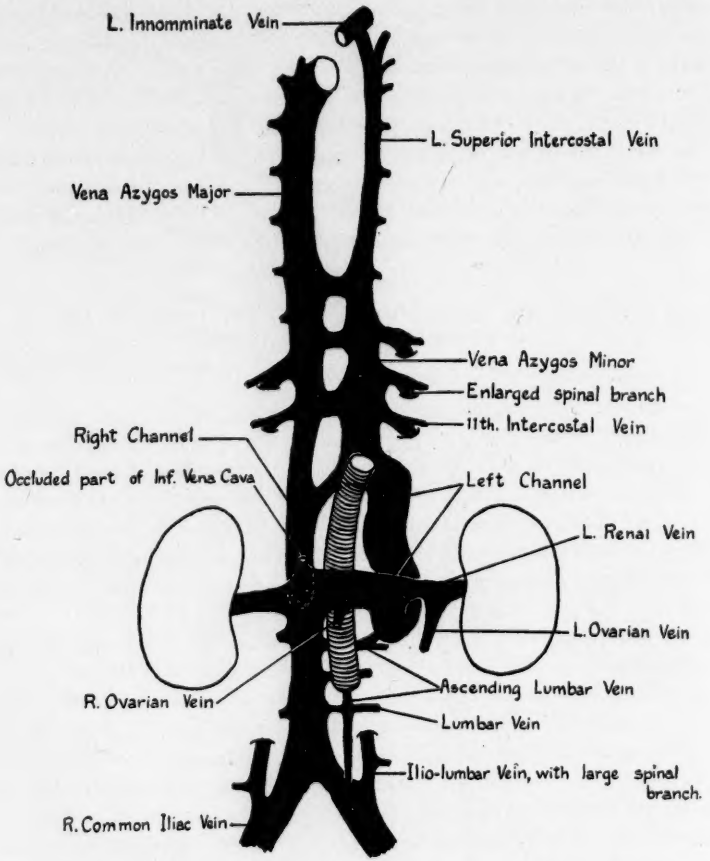


Fig. 5. The principal veins in Case 4 (Case of obstructed hepatic portion of inferior vena cava).

point where it turned downwards from its transverse part, the left renal vein, which had already received the left ovarian vein; and (3) at the point where it doubled back on itself in order to ascend, the ascending lumbar vein, which was of small size.

The vena azygos minor and the left superior intercostal vein together

formed a continuous vessel which gradually diminished in diameter from below up, and which received the eleven intercostal veins of the left side. The spinal branches of these intercostal veins were much enlarged.

The ilio-lumbar veins were large, especially the spinal branches. In the lumbar portion of the vertebral canal there were large venous channels lying outside the dura mater and on either side of the posterior common ligament. All the enlarged spinal branches mentioned were continuous with these channels. Blood evidently passed from the common iliac veins to the ilio-lumbar veins, and along their spinal branches to the spinal branches of the intercostal veins by way of the vessels in the vertebral canal; a route was thus provided by which some of the blood from the lower extremities reached the superior caval system.

Large veins were also observed in the ventral abdominal wall, suggesting that blood may also have passed by way of the epigastric veins to the superior vena cava.

### *Developmental Interpretation*

Viewing this case as a whole, we find that we have present two distinct groups of features.

*On the one hand,* there is continuity of the inferior vena cava, through the right and left channels described above, with the vena azygos major and the vena azygos minor respectively. This condition is due to enlargement of both the thoracic supracardinals, and has doubtless persisted from the early embryonic stage at which these were continuous with the lumbar supracardinals. To explain this condition it is necessary, we believe, to assume that some obstruction, incomplete and possibly temporary, of the hepatic part of the inferior vena cava was present at the early embryonic stage just mentioned. This explanation also accounts for the continuity of the vena azygos minor with the left superior intercostal vein, this continuous channel being necessary for the conveyance of blood back to the heart.

The principal vessels present are interpreted as follows in terms of their embryological constituents (fig. 1): The postrenal part of the inferior vena cava is normal and includes the right lumbar supracardinal. The right channel, including the vena azygos major, consists of (1) the right thoracic supracardinal and (2) the cranial end of the right postcardinal. The left channel may be regarded as formed by (1) the right supracardino-subcardinal anastomosis, (2) the intersubcardinal anastomosis, (3) the left supracardino-subcardinal anastomosis, (4) the left thoracic supracardinal, and (5) the cranial end of the left postcardinal. The transverse anastomoses connecting the vena azygos major and the vena azygos minor represent four of the thoracic intersupracardinal anastomoses which have persisted.

*On the other hand,* we have present (1) the fibrous cord representing the obliterated part of the inferior vena cava, and (2) the enlarged spinal and abdominal veins. These features, especially the latter, are characteristic of

inferior caval obstruction[1] and together point to the obstruction having become complete and permanent either postnatally or at any rate in later foetal life. Had permanent obstruction occurred at the early embryonic period at which the lumbar and thoracic supracardinals were continuous, the obstructed part would, as is characteristic of both arteries and veins which disappear at such early periods, have become absorbed completely and could not have persisted as a fibrous cord showing traces of a lumen.

In this case, therefore, we believe (1) that incomplete and possibly temporary obstruction of the hepatic part of the inferior vena cava occurred at an early embryonic stage and resulted in the right and left channels connecting the inferior vena cava with the azygos veins; and (2) that either postnatally or at some late stage *in utero* the obstruction became complete and permanent, resulting in the enlargement of the superficial abdominal and spinal veins and probably also in further enlargement of the persistent developmental connections.

## BIBLIOGRAPHY OF ANOMALIES OF THE INFERIOR VENA CAVA AND AZYGOS VEINS IN MAN

In studying and classifying anomalies of the inferior vena cava, it has been found impossible to exclude entirely anomalies of the azygos system, owing to the close developmental relationship of the two systems. An attempt has been made to classify the cases as left inferior vena cava, double inferior vena cava, etc., but here again, it is difficult to define the different types. For this reason some overlapping will be observed, and the cases have been placed in what seems the most suitable class. Those cases that cannot definitely be placed in one or the other of the following groups have been placed at the end under the title, "Miscellaneous," often because the details were insufficient, or because the original descriptions were not available.

*Double Inferior Vena Cava*

(1) Cambridge Anomaly Book. See *Journal of Anatomy and Physiology*, vol. XXXV, p. 123.
Case 1. Double postrenal inferior vena cava with small communication with vena azygos major. Case 2. Double postrenal inferior vena cava.

(2) GÉRARD, G. (1903). *Bibliogr. Anat.* t. XII, p. 293; see *Anat. Anzeig.* Bd. XLIII, S. 347.
Apparently double inferior vena cava (no further details available).

(3) GORRON (1900). *Bull. Soc. Anat. de Paris*, p. 691. (See *Journ. Anat. and Physiol.* vol. XXXV, p. 504.)
Double inferior vena cava.

(4) KOLLMAN, J. *Anat. Anzeig.* Bd. VIII, S. 97.
Double inferior vena cava (good bibliography).

(5) —— *Anat. Anzeig.* Bd. VIII, S. 104.
Double inferior vena cava continuous with vena azygos minor which joins vena azygos major in usual way.

(6) LUCAS, M. F. *Journ. of Anat.* vol. LI, p. 69.
Double postrenal inferior vena cava.

(7) MARTIN (1852). *Monatschrift für Geburtskunde*, Bd. XX. See *Journ. of Anat. and Physiol.* vol. XXXV, p. 13.
Persistence of thoracic and lumbar cardinals in each side. (It is not clear whether postcardinals or supracardinals.)

[1] For an excellent and extensive account of inferior caval obstruction, see article by J. Hall Pleasants in *Johns Hopkins Hospital Reports*, vol. XVI, p. 363.

(8) Melissinos. *Anat. Anzeig.* Bd. xxxix, S. 149.
Double postrenal inferior vena cava, both trunks on the right side, right supracardinal and right postcardinal persistent.
(9) Nicolai, N. (1886). *Diss. med. Kiel.* See *Anat. Anzeig.* Bd. xliii, S. 348.
Two cases of partial doubling of inferior vena cava.
(10) Osler, W. *Journ. of Anat. and Physiol.* vol. xiii, p. 291.
Postrenally, double inferior vena cava. Prerenally, obliteration of hepatic portion of inferior vena cava; blood reaches heart via azygos system.
(11) Pangratz (1894). *Ueb. d. sogen. Verdoppelung d. ob. und unt. Hohlvene.* Konigsberg.
(12) Patten, C. J. *Anat. Anzeig.* Bd. xxxiv, S. 189.
Double postrenal inferior vena cava.
(13) Rischbieth, H. *Journ. of Anat. and Physiol.* vol. xlviii, p. 287.
Double postrenal inferior vena cava.
(14) Shepherd, F. J. *Journ. of Anat. and Physiol.* vol. xxiv, p. 71.
Double postrenal inferior vena cava.
(15) Walter, J. (1884). *Diss. med. Erlangen.* See *Anat. Anzeig.* Bd. xliii, S. 348.
Partial doubling of inferior vena cava.
(16) Wallin, I. E. *Anat. Rec.* vol. xx, p. 95.
Double postrenal inferior vena cava.
(17) Waterston, D. *Journ. of Anat. and Physiol.* vol. xlvii, p. 433.
Double inferior vena cava.
(18) Stieda, L. *Anat. Anzeig.* Bd. viii, S. 655.
(19) Gruber, W. (1859). *Mém de l'Acad. Imp. des sc. de St Pétersbourg,* t. ii, p. 25. See *Anat. Anzeig.* Bd. viii, S. 113.
(20) —— (1880). *Arch. f. path. Anatomie,* Bd. lxxxi, S. 465. See *Anat. Anzeig.* Bd. viii, S. 113.
(21) —— (1881). *Arch. f. path. Anatomie,* Bd. lxxxvi, S. 493. See *Anat. Anzeig.* Bd. viii, S. 113.
(22) Kadyi (1881). *Wiener med. Jahrbücher,* Jahrgang, S. 40. See *Anat. Anzeig.* Bd. viii, S. 114.
(23) Zagorsky, P. (1822). *Mém. de l'Acad. Imp. des sc. de St Pétersbourg,* t. viii, S. 288. See *Anat. Anzeig.* Bd. viii, S. 116.
(24) Lauber, H. *Anat. Anzeig.* Bd. xix, S. 590. See also *Journ. of Anat. and Physiol.* vol. xxxvi, p. 305.
Double postrenal inferior vena cava with small normal prerenal inferior vena cava. The main channel by which blood reaches the heart is an enlarged vena azygos major.

*Left Inferior Vena Cava*

(1) Alten, V. *Anat. Anzeig.* Bd. xliii, S. 337.
A case similar to that described by us. The small persistent right supracardinal is in addition continuous with the vena azygos major.
(2) Dorsch (1858). *Bayer. Aerz. Intelligenzblatt,* no. 20. See *Journ. of Anat. and Physiol.* vol. xxxv, p. 15.
Left prerenal and postrenal inferior vena cava continuous.
(3) Frankel, W. *Anat. Anzeig.* Bd. xxxvii, S. 240.
Left postrenal inferior vena cava.
(4) Georg, H. (1906). *Diss. med. München.* See *Anat. Anzeig.* Bd. xliii, S. 347.
Persistent left cardinal.
(5) Gérard, G. (1906). *Bibliogr. Anat.* t. xv, p. 85. See *Anat. Anzeig.* Bd. xliii, S. 347.
Persistent left postrenal cardinal (we have not been able to ascertain whether supracardinal or postcardinal).
(6) Gladstone, R. J. *Journ. of Anat. and Physiol.* vol. xlvi, p. 220.
Left postrenal inferior vena cava crossing over and becoming normal prerenally. There are also two small vessels running between inferior vena cava and vena azygos major.
(7) Grimsdale. *Journ. of Anat. and Physiol.* vol. xxviii, p. 5.
Left postrenal inferior vena cava.
(8) M'Whinnie (1840). *London Med. Gaz.* March 27th, p. 31. See *Journ. of Anat. and Physiol.* vol. xxxv, p. 15.
The two common iliac veins unite at first lumbar level on the left side and resultant vessel continues on the left side. Situs inversus viscerum.

(9) Neuberger, H. *Anat. Anzeig.* Bd. xliii, S. 65.
Left postrenal inferior vena cava becomes continuous with vena azygos major.

(10) Paterson, A. M. *Journ. of Anat. and Physiol.* vol. xxxv, p. lviii.
Left postrenal inferior vena cava crossing over to become normal prerenal inferior vena cava. There is also a vessel connecting the two renal veins behind the aorta.

(11) Rahman, M. A. *Journ. of Anat.* vol. li, p. 307.
Left prerenal and postrenal inferior vena cava with transposition of viscera.

(12) Revell, D. G. *Amer. Journ. of Anat.* vol. ii, p. xvi.
Left postrenal inferior vena cava joining up with vena azygos minor, crosses over to join vena azygos major in usual way. Also there was a small postrenal supracardinal.

(13) Struthers. *Journ. of Anat. and Physiol.* vol. xxvii, p. vi.
Left postrenal inferior vena cava crossing to become normal prerenal inferior vena cava.

(14) Waring, H. J. *Journ. of Anat. and Physiol.* vol. xxviii, p. 46.
Similar to case above (no. 13).

*Combined Anomalies of Inferior Vena Cava and Azygos System*

(1) Abernethy (1793). *Phil. Trans. Royal Soc. London*, pt. 1.
Persistent right cardinal probably continuous with azygos system.

(2) Carpentier and Bertaux (1888). *Arch. de Physiol. norm. et path.* p. 79.
Persistent right cardinal. Prerenal inferior vena cava continuous with azygos system.

(3) Cruveilhier. *Traité d'Anatomie Descriptive*, t. iii, 4th ed. p. 223.
Normal postrenal inferior vena cava crossing to left prerenally, and becoming continuous with an enlarged vena azygos minor which again crosses to right to enter vena azygos major in the usual manner.

(4) Horner (1817 and 1818). *Journ. of Acad. of Philadelphia.*
Same as no. 2 (case of Carpentier and Bertaux).

(5) Kampmeier, O. F. *Anat. Record*, vol. xix, p. 361.
Occlusion of right auricle resulting in complete closure of mouth of superior vena cava, so that blood flowed down via azygos system to enter inferior vena cava at level of diaphragm.

(6) Klob (1859). *Zeitschrift d. Kaiser. Gesellsch. der Aerzte zu Wien*, Bd. xv, S. 733, vide Schmidt's *Jahrbücher.*
Persistent right cardinal probably continuous with vena azygos major.

(7) Paulus (1842). *Ost. Med. Wochenschrift*, Bd. ii, S. 313, vide Canstatt's *Jahresbericht.*
Same as no. 6 (Klob's case).
*Note.* For no.'s 1, 2, 3, 4, 6, and 7, see T. Dwight's article, *Journ. of Anat. and Physiol.* vol. xxxv, p. 7.

*Miscellaneous*

(1) Cambridge Anomaly Book. See *Journ. of Anat. and Physiol.* vol. xxxv, p. 124, no. 3.
Normal inferior vena cava with small persistent left supracardinal.

(2) Cambridge Anomaly Book. See *Journ. of Anat. and Physiol.* vol. xxxv, p. 124, no. 4.
Inferior vena cava normal as far as liver where it was greatly contracted and reached the heart as a very small vein. Main channel for blood was via vena azygos major with which inferior vena cava was continuous.

(3) Cameron, J. *Journ. of Anat. and Physiol.* vol. xlv, p. 416.
Normal inferior vena cava with small persistent left supracardinal.

(4) Dwight, T. *Journ. of Anat. and Physiol.* vol. xxxv, p. 7.
Left inferior vena cava continuous with vena azygos minor, which crossed as usual to join vena azygos major, which however was much enlarged as was the vena azygos minor.

(5) Gérard, G. (1908). *Bibliogr. Anat.* t. xvii, p. 227. See *Anat. Anzeig.* Bd. xliii, S. 347.
Unusual anomaly of the inferior vena cava.

(6) Gerlach, L. (1885). *Sitz. der Physic. med. Societät zu Erlangen.* Sitz. V. 12 Jan. 1885. See *Anat. Anzeig.* Bd. viii, S. 113.

(7) Gladstone, R. J. *Journ. of Anat.* vol. xlv, p. 225.
Persistent true postcardinal with ureter passing round it.

(8) GRIFFITH, T. W. See *Journ. of Anat. and Physiol.* vol. XXXIII, p. 503. Article is in the "Scalpel" for Jan. 1899, vol. IV, p. 13.
Description of two cases of obstructed inferior vena cava, in one of which blood was returned to the heart via azygos system.

(9) —— *Journ. of Anat. and Physiol.* vol. XXVI, p. 117.
Absence of hepatic portion of inferior vena cava. Blood returned to the heart via azygos system. Also situs inversus viscerum.

(10) HOCHSTETTER (1893). *Morph. Jahrbüch.* Bd. XX. See *Journ. of Anat. and Physiol.* vol. XXXV, p. 15.

(11) JOHNSTON, T. B. *Journ. of Anat. and Physiol.* vol. XLVII, p. 235.
Normal right inferior vena cava with small persistent left supracardinal.

(12) KOLISKO, F. *Anat. Anzeig.* Bd. XXXIV, S. 520.
Right ureter passing round a persistent right postcardinal.

(13) LAWRENCE, T. W. P. and D. NABARRO. *Journ. of Anat. and Physiol.* vol. XXXVI, p. 63.
Absence of hepatic portion of inferior vena cava.

(14) PONSOT, J. (1857). *Mémoires de la Soc. de Biologie*, 1856, p. 195, Paris. See *Anat. Anzeig.* Bd. VIII, S. 115.

# CONCERNING THE HOMOLOGIES OF THE HYOMANDIBULA AND PREOPERCULUM

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The term "hyomandibula" is employed to designate an element of the hyal arch which articulates by its proximal end with the neurocranium, and by its distal end supports the palatoquadrate either directly or indirectly through the intermediation of a symplectic. The articulation with the neurocranium is always with the otic capsule, and because of this the hyomandibula permits a swinging motion of the distal end of the palatoquadrate, this motion being backward and forward and upward and downward and hence necessarily inward and outward.

The hyomandibulae of all Fishes have up to recent times been generally considered to be homologous, Gegenbaur (1872) being the great exponent of this theory. My work long ago led me to doubt the homology of these structures, and in two works, published the one in 1915 the other in 1918, I stated my conviction that the hyomandibula of the Selachii was an epihyal, that of the Batoidei a pharyngohyal, that of the Chondrostei a bar formed by the fusion of certain of the dorsal ones of the anterior row of branchial rays of the hyal arch, and the hyomandibula of the Holostei and Teleostei that same anterior branchial-ray bar fused with a similar bar developed from the posterior row of branchial rays of the same arch. It was shown that in all of the Plagiostomi up to that time described in this connection, the hyomandibula articulates with the otic capsule ventral to the vena jugularis and ramus hyomandibularis facialis, while that of the Teleostomi articulates with that capsule dorsal to that vein and nerve, and the relations to this vein and nerve were considered to be of such morphological significance that they definitely establish the non-homology of the hyomandibulae of these two groups of Fishes.

If Gegenbaur's theory is correct, any one of my four types of hyomandibula could be directly derived from any one of the other three. If, on the contrary, my theory is correct, the teleostean hyomandibula might have been derived from the chondrostean by the later addition to it of a posterior branchial-ray bar, and the chondrostean type might have been developed from the teleostean by the suppression of that bar, but a Fish possessing a functional hyomandibula of either the teleostomian, selachian or batoidean type could not have been descended from a Fish possessing either of the other two unless, at some-time in the intervening interval, the hyomandibula of this ancestor had ceased

to be functional. When the skull is autostylic, cartilages representing one or more of my four types of hyomandibula might be present but necessarily non-functional.

Schmalhausen (1923), in the earliest discussion of this subject since the publication of my two works above referred to, considers the hyomandibulae of all Fishes to be epihyals, and hence all homologous, the pharyngohyal in each case either having completely aborted or having completely fused with the epihyal. He recognises that the hyomandibula of the Selachii articulates with the otic capsule ventral to the vena jugularis and ramus hyomandibularis facialis, and that that of the Teleostomi articulates with that capsule dorsal to that vein and nerve; and to explain this marked difference in the relations of the hyomandibula to this vein and nerve he suggests that the hyomandibula of the Teleostomi may have had primarily a double articulation with the otic capsule, one ventral and the other dorsal to the jugular vein, but it is evident that as long as this double articulation persisted the hyomandibula would have been incapable of its characteristic swinging motion inward and outward.

Stensiö (1925 *b*) considers the hyomandibula of the Teleostomi to have been directly derived from that of the Selachii by the simple shifting of its surface of articulation with the otic capsule from a position ventral to the vena jugularis and ramus hyomandibularis facialis to one dorsal to that vein and nerve, this being rendered possible by the enclosure of the vein and nerve in a canal in the lateral wall of the neurocranium. This possibility was carefully considered by me in the works above referred to and considered untenable and will be later again referred to.

De Beer, in a work published in 1924, accepted with slight modification my theory of the development of the teleostomian hyomandibula, but he still followed Gegenbaur in considering the hyomandibula of the Selachii to represent the dorsal portion of the hyal bar, and he apparently included the Batoidei under the term Selachii as Gegenbaur did. In a later work (1926) he changes his opinion regarding the teleostomian hyomandibula and states his adhesion to Stensiö's suggestions above referred to, but he says it was first suggested to him by Prof. Goodrich.

Edgeworth, in the most extensive discussion of this subject (1926), states his full and unqualified adhesion to Gegenbaur's theory that the hyomandibulae of all Fishes are homologous and represent the dorsal portion of the hyal bar. He says that the hyal bar in all Fishes first appears as a continuous rod of cartilage lying at some distance from the neurocranium. Later it grows upward toward the neurocranium and acquires articulation with the lateral surface of the otic capsule at some point between the floor of the capsule and its dorso-lateral edge, the point of articulation apparently being considered to be fortuitous and hence unimportant. The relations of the bar to the vena jugularis are apparently also considered to be fortuitous, for he says (1926, p. 191) that the vena jugularis lies "external to the hyomandibula in *Scyllium*, this relationship is not constant in the Selachii. Thus the vein is dorso-external to

the cartilage in *Acanthias* and *Mustelus* and dorsal to it in *Heptanchus*." In both of these fishes, however, the vein lies external to the hyomandibula, which alone is important in this connection, and he cites no single instance in which it lies ventral to the hyomandibula in the Selachii or dorsal to it in the Teleostomi. The hyomandibula is said to be segmented off from the dorsal portion of this bar and in the Selachii and in *Ceratodus* is postfacialis in position, but in the Teleostomi prefacialis. In certain of these latter fishes (Holostei, Teleostei), Edgeworth says that there is a process-like outgrowth from the hind edge of the prefacialis hyomandibula which first surrounds and encloses the ramus hyomandibularis facialis and then extends posteriorly to form the entire postfacialis portion of the teleostean hyomandibula which is often more important than the prefacialis portion. He found no evidence in any of his specimens of an independent cartilage that could correspond to my posterior branchial-ray bar, and he also found no indication of the articulation of the hyomandibula with the otic capsule having shifted upward from a position ventral to the vena jugularis and ramus hyomandibularis facialis to one dorsal to that vein and nerve.

The several authors above referred to apparently either overlook the fact that there is in the recent Batoidei a fully developed and wholly independent cartilage that certainly corresponds to some part of the epihyal of other Fishes and lies morphologically ventral to the hyomandibula, and that in several of the recent Selachii there is a rudimentary pharyngohyal lying morphologically dorsal to the hyomandibula (Luther, Allis, Sewertzoff), or they do not accept my interpretation of the homologies of these cartilages.

### *CERATODUS*

Edgeworth, in the work above referred to, describes the conditions in early embryos of *Ceratodus* and there refers to the dorsal half of the hyal bar as the epihyal. This part of the bar is there said to segment into three parts, the dorsal one of which he calls the otoquadrate, the next following one the interhyal, and the ventral one the hyosuspensorial ligament. The otoquadrate is said to extend from the ventral surface of the otic capsule to the quadrate and later to fuse with each of these two cartilages. He does not say in this work with what part of the quadrate the otoquadrate fuses, but in an earlier work (Edgeworth, 1923) it is said to "join" the inner surface of the otic process of the palatoquadrate. The otoquadrate is said to lie ventral to the vena jugularis and ramus hyomandibularis facialis, and it certainly lies dorsal (external) to the lateral dorsal aorta. The hyal bar has acquired the Σ-shape, the otoquadrate being directed latero-ventro-anteriorly, the interhyal and suspensorial ligament ventrally and slightly posteriorly, and the ceratohyal ventro-antero-mesially.

The otoquadrate of the above descriptions is thus certainly a pharyngohyal and the corresponding cartilage is so designated by Schmalhausen in his descriptions of this fish, the interhyal and hyosuspensorial ligament together

forming the epihyal. No other cartilages related to this arch are here described by Edgeworth, but two such cartilages have been described by several authors, and even by Edgeworth himself in an earlier work (1923), one of these cartilages being prefacialis and the other postfacialis in position.

The prefacialis cartilage above referred to is said by Krawetz (1910) to be a process which arises from the distal end of the pharyngohyal, projects dorsally lateral to the vena jugularis and the ramus hyomandibularis facialis, and ultimately acquires contact with the so-called otic process of the palatoquadrate. Edgeworth (1911, p. 213) says that this cartilage is a downgrowth from the outer edge of the otic capsule which segments off and acquires contact with the distal end of the pharyngohyal, this cartilage thus evidently forming a bar which extends from the latter cartilage to the lateral wall of the otic capsule, dorsal to the vena jugularis and ramus hyomandibularis facialis. Sewertzoff (1902) had previously described this cartilage as an independent prefacialis cartilage and Schmalhausen has recently described it as such, saying that it lies lateral to the vena jugularis and is the homologue of Huxley's hyomandibula of the adult. Edgeworth, however, in his recent work (1926, p. 174), says that the cartilage so described by Schmalhausen is simply the slightly downturned lateral edge of the otic capsule, and adds that in none of the specimens examined by him in connection with his work is this lateral edge segmented off. This little cartilage is therefore said to be of independent extracranial origin in certain specimens, of visceral origin in others, of cranial origin in still others and in certain specimens to be wholly absent. It is therefore quite certain that this cartilage was developed from cells that lay primarily between the otic capsule and the distal end of the pharyngohyal and that in certain specimens it first fused with the otic capsule and in others with the pharyngohyal, and in recent Fishes there are no cartilaginous cells that have these relations to these two cartilages (otic capsule and pharyngohyal) excepting only the dorsal ones of the branchial rays of the anterior row of the hyal arch.

The postfacialis cartilage above referred to is described by several of these authors, but is simply said to lie posterior to the ramus hyomandibularis facialis and external to the vena jugularis. Ultimately it comes into relation with the operculum (Schmalhausen, 1923), thus giving origin to the several little cartilages of the adult said by Huxley (1876) to be related to the operculum and interoperculum, the larger one giving articulation to the former bone and the next larger one to the interoperculum. These little cartilages are generally considered to have been derived from branchial rays of the hyal arch (Goodrich, 1909), and hence represent some part of my posterior branchial-ray bar.

The pharyngohyal and epihyal of embryos of this fish are thus seen to have retained their primitive relations to the pharyngobranchial membrane, lying directly internal to it, and two extracranial cartilages have been developed, one prefacialis and the other postfacialis in position, which represent my anterior and posterior branchial-ray bars. The pharyngohyal strikingly resembles in topographical position the hyomandibula of the Batoidei and is

quite certainly the homologue of that cartilage. In *Torpedo marmorata* a hook-like process arises from the distal end of the hyomandibula (see Allis, 1915, pp. 586–91) which is evidently the homologue of the prefacialis process of Krawetz's descriptions of embryos of *Ceratodus*. This process is said by de Beer (1926) to be indicated in a 24 mm. embryo of this fish by dense mesenchyme. In *Narcine* this process is represented by a wholly independent piece of cartilage. From the dorsal end of the process of *Torpedo occellata* a ligament extends dorsally, external to the vena jugularis and ramus hyomandibularis facialis, and is inserted on the otic capsule dorsal to that vein and nerve. I formerly considered this ligament to represent the levator muscle of the hyal arch, but it seems quite unquestionable that it and the process together represent the prefacialis cartilage of embryos of *Ceratodus*. In the Selachii this ligament of *Torpedo* is represented by the superior postspiracular one, and in *Mustelus* and *Heptanchus* I found this ligament in part attached to the posterior wall of the spiracular canal, this evidently suggesting a derivation from tissues related to the branchial rays of the anterior row of the hyal arch. In certain fishes this ligament chondrifies in part and I suggested (Allis, 1901, pp. 193–4), even at that early date, that this ligament might represent the prefacialis portion of the teleostean hyomandibula.

### *MACROPETALICHTHYS*

Stensiö, in the work referred to in the earlier part of this paper, describes the neurocranium of *Macropetalichthys rapheidolabis*, a fossil Arthrodira. The neurocranium of this fish is broad and flat, and the head of the fish must have resembled that of the recent Batoidei, with the eyes situated on the dorsal surface of the head not far from its lateral edges. The dorsal surface of the head is covered by a shield of dermal bone, which Stensiö calls "the dermal cranial roof." The postorbital portion of this dermal cranial roof projects latero-ventrally in a curved line and covers a large part of the cheek, corresponding in position to the postorbital and suborbital bones of *Amia* fused with each other and with the lateral edges of the dermal bones on the dorsal surface of the head.

The cranial portion of the latero-sensory canals of *Macropetalichthys* is completely enclosed in the shield-like dermal cranial roof. There are main latero-infraorbital, supraorbital and supratemporal canals, and a branch canal arises from the infraorbital canal between its postorbital and suborbital portions. That part of the infraorbital canal that lies anterior to this branch canal is innervated by the nervus facialis, the part that lies posterior to the branch canal being said by Stensiö to be probably innervated by the nervus glossopharyngeus. Because of this assumed innervation of the postorbital portion of the infraorbital canal by the glossopharyngeus, Stensiö considers the branch canal to arise from the main latero-infraorbital canal between its preauditory and postauditory portions, and hence to be the homologue of the preopercular canal of recent bony Fishes, which is said to always have that origin from the main canal. The branch canal is therefore called by him the preopercular.

This homologisation of the branch canal of *Macropetalichthys* and the assumed innervation of the postorbital portion of the infraorbital canal by the nervus glossopharyngeus both seem to be in error.

In both *Chlamydoselachus* and *Laemargus* a branch canal arises from the infraorbital between its postorbital and suborbital portions and runs posteriorly across the cheek, thus having to the infraorbital canal exactly the topographical relations of the branch canal of *Macropetalichthys*. This canal of *Chlamydoselachus* is called by Garman (1888) the angular + jugal. The canal in *Laemargus* is called by Ewart (1892) the hyomandibular, and that part of the infraorbital canal that, in both these fishes, lies dorsal to this branch canal is innervated by the rami buccalis and oticus lateralis and not by the nervus glossopharyngeus. In *Amia calva* this canal of these fishes is represented by the horizontal cheek-line of pit organs of my descriptions (Allis, 1889), and that part of the infraorbital canal that lies dorsal to the anterior end of this line is innervated as it is in *Chlamydoselachus* and *Laemargus*, by the rami buccalis and oticus lateralis. From the hind end of the angular canal of *Chlamydoselachus* a branch canal runs downward on the cheek and then forward on the mandible and is called by Garman the oral. It is the homologue of the vertical cheek + mandibular lines of pit organs of *Amia*, and this line and the angular line of *Chlamydoselachus* together form a curved line which lies external to the skeletal bar of the mandibular arch. Posterior to this line, there is in *Chlamydoselachus* a long curved latero-sensory groove which begins slightly posterior to the spiracle and ends near the tip of the mandible (Allis, 1923 *b*). This groove lies throughout its entire length external to or slightly posterior to the skeletal bar of the hyal arch, for although the ventral portion of this groove actually runs on to the external surface of the mandible it nevertheless lies external to the ventral end of the hyal arch, that end of the arch here lying internal to the mandible. In *Mustelus* this sensory groove is represented by a line of large surface sense organs (Allis, 1901), and this line and the groove of *Chlamydoselachus* are certainly the homologues of the preoperculo-mandibular canal of recent bony fishes.

In *Chimaera monstrosa* Garman (1888) says that one or two canals arise from the infraorbital between its postorbital and suborbital portions and they separate into three branches, a jugal which runs posteriorly across the cheek, an oral which runs to the lower jaw, and an angular which runs forward in the upper jaw. These same canals are shown by Cole (1896) in this fish, the jugal and oral here being called by him the hyomandibular, and the angular being considered to be a part of the infraorbital canal. These canals evidently correspond to the canals above described in *Chlamydoselachus* and *Laemargus*, and that part of the infraorbital canal that lies dorso-posterior to them is innervated, as in the latter fishes, by the rami buccalis and oticus lateralis. In *Ceratodus*, van Wijhe (1882) describes two canals in the same region, one of them having the course of the angular + oral of *Chlamydoselachus* and the other running forward in the lower lip. Van Wijhe does not name these canals nor

does he give their innervation, but they are evidently the homologues of the canals of *Chlamydoselachus* and *Chimaera*, and as van Wijhe describes a ramus oticus in this fish, it evidently innervates some portion of the infraorbital canal that lies dorsal to these branches of that canal.

Comparison of the conditions in *Macropetalichthys* with those in the several fishes above referred to therefore leaves little doubt that the so-called branch canal of the former is the homologue of the angular+jugal or hyomandibular canal of the latter fishes, and as these latter canals are certainly the homologues of the horizontal and vertical cheek-lines of pit organs of *Amia*, I shall hereafter refer to them as the cheek-line canal which may have two components, a horizontal and a vertical one. The bone related to this canal, if there be one, will be called the cheek-line bone.

The latero-sensory canals of *Macropetalichthys* are, as already stated, wholly enclosed in the bone of the dermal cranial roof, they are fine, with numerous delicate unbranching tubules leading to the outer surface, and in this respect as well as in their distribution on the cheek of the fish they are apparently of the selachian type. The tubules are arranged in two parallel rows along each canal, as they also are in certain others of the Arthrodira and in the Ostracoderma. This arrangement of the tubules is not known in any of the recent bony fishes, but is found along the so-called nasal canal of Garman's descriptions of the Selachii. The nasal canal of the latter fishes lies on the ventral surface of the snout between the nasal capsules, and is formed by the fusion of short sections of the infraorbital canals of opposite sides of the head, the tubules not taking part in this fusion and persisting as two parallel rows of tubules one along either side of the canal. This suggests that there may have been two parallel and closely adjacent sensory lines in *Macropetalichthys*. Two such lines are actually found along certain of the canal lines in embryos of *Spinax niger* and also in embryos of *Amia calva*, one of these lines in *Spinax niger* being said by Ruud (1920) to give origin to the latero-sensory organs and the other to ampullary organs, while the second one of the corresponding lines in *Amia* gives origin to terminal buds (Allis, 1889). There are no perforations of the dermal cranial roof of *Macropetalichthys* that could have transmitted ampullary tubules, ampullary organs thus certainly not having developed in this fish to the extent that they have in the recent Selachii.

The postorbital process of the chondrocranium of *Macropetalichthys* has grown latero-ventrally and then anteriorly and underlies throughout their full extent the postorbital and suborbital portions of the dermal cranial roof, the morphologically lateral surface of the process being presented ventrally and lying in the plane of the ventral surface of the neurocranium. The jugular vein, as it runs posteriorly along the lateral surface of the neurocranium, is enclosed in a canal which traverses the postorbital process, the anterior opening of this canal lying on the anterior surface of the process, close to the lateral (morphologically dorsal) edge of its ventral (morphologically lateral) surface. Slightly posterior to the anterior opening of this canal, a branch canal is sent dorso-

mesially and opens in the orbit. The direction of this branch canal indicates that the vein it transmitted ran antero-mesially dorsal to the nervus trigeminus and the muscles of the eyeball and joined the ramus ophthalmicus superficialis, thus being the ophthalmic vein of my descriptions of *Polypterus* (Allis, 1922 *a*). Stensiö concluded that this branch canal transmitted the main jugular vein, the anterior prolongation of the jugular canal simply transmitting the mandibular vein. But it is much more probable that this anterior prolongation of the canal transmitted the anterior prolongation of the jugular vein formed by the union of the mandibular and suborbital (orbitonasal) veins. Whether or not there was a pituitary vein Stensiö could not determine. He found no pituitary foramen traversing the cranial wall, and it is quite possible that in this fish as in *Ameiurus*, the pituitary region was drained by an intracranial vein which ran posteriorly and issued through the vagus foramen (Allis, 1908).

Posterior to the canal that transmits the ophthalmic vein the jugular canal becomes connected by a sinus with a canal that transmits the lateral dorsal aorta (arteria carotis int.), and here two branches are given off by the jugular canal which open on the outer surface of the process by a single opening, that opening lying not far from the posterior edge of the ventro-lateral surface of the postorbital process. One of these canals is considered by Stensiö to have transmitted the vein of the hyal arch, and the other the efferent artery of that arch.

There is in the cranial cavity of *Macropetalichthys* a recessus acusticofacialis and a recessus trigeminus, separated from each other by a thick wall of cartilage. The recessus acusticofacialis lodges the ganglion of the nervus facialis and from it a long canal arises which transmits the nervus facialis. Branches of this canal transmit the nervi ophthalmicus, buccalis and palatinus, the remainder of the canal, which transmits the ramus hyomandibularis, then opening on the ventro-lateral surface of the postorbital process slightly mesial (morphologically ventral) to the anterior opening of the jugular canal. What the course of the ramus hyomandibularis facialis was after issuing from its canal Stensiö could not determine from his specimens, but he suggests that it may have traversed the jugular canal. There is, however, nothing to definitely show that such was the case.

Stensiö found no trace of a hyomandibula in any of his specimens of *Macropetalichthys* and no trace on the neurocranium of an articular facet related to it. He however concludes that there was a hyomandibula in this fish, that it was the homologue of that of the Selachii, and that it either had acquired articular relations with the neurocranium anterior to the external opening of the two little canals which he believes to have transmitted the vein and efferent artery of the hyal arch, or that it was there attached by ligament. The articular surface would thus lie wholly on the ventro-lateral surface of the postorbital process at its extreme dorso-lateral edge, and, as shown in his figures, dorso-lateral to the jugular canal or partly upon the external surface of the lateral wall of that canal.

Stensiö therefore considers the conditions in this fish to represent an intermediate stage in the shifting of the articulation of the hyomandibula from a position ventral to the vena jugularis and ramus hyomandibularis facialis to one dorsal to that vein and nerve, the teleostean hyomandibula thus being directly derived from the selachian. This possibility was, as already stated, considered in my earlier work (Allis, 1915) and rejected as untenable, and the conditions in *Macropetalichthys* are in my opinion favourable instead of unfavourable to this conclusion; for the following reasons:—

1. The simple shifting of the hyomandibula from a position ventral to the vena jugularis and ramus hyomandibularis facialis to one dorsal to that vein and nerve would not in any way entail a change of other selachian features to non-selachian ones. This supposition therefore presupposes either that a non-selachian fish had already acquired a selachian hyomandibula, or that a selachian fish acquired and retained for a certain time a teleostean one, and no teleostean fish is known, either recent or fossil, in which the hyomandibula lies ventral to the vena jugularis and ramus hyomandibularis facialis, and no selachian in which it lies dorsal to that vein and nerve.

2. It is highly probable that there was no functional hyomandibula in this fish, as there certainly was none in the crossopterigian *Wimania*, to be described below.

3. The rigid bony covering of the cheek of *Macropetalichthys* was markedly unfavourable to the development and even to the presence of a hyomandibular suspensorium of any type whatever, for it would permit but little of that inward and outward swinging of the cheek that is a characteristic feature of the proper functioning of such a suspensorium.

4. But admitting that there was a hyomandibula of the selachian type in the ancestors of this fish, if it were to acquire the articulation that Stensiö ascribes to it, on the actually ventro-lateral corner of the postorbital process, it would lie in a nearly vertical longitudinal plane and definitely lateral to the spiracular canal, and hence morphologically anterior to it. There is no spiracular perforation of the dermal cranial roof, the spiracular opening, if present, therefore probably lying posterior to the ventro-laterally projecting postorbital portion of the dermal cranial roof.

5. A pharyngohyal, symplectic and interhyal would have to be in some way accounted for.

6. If the ramus hyomandibularis facialis traversed the jugular canal, as Stensiö suggests, its ramus mandibularis, which in recent Fishes always accompanies the ramus hyoideus in its passage through the canal, would run outward posterior to the hyomandibula, and it would be difficult to explain how it could acquire the position that it has in *Polypterus*, anterior to the hyomandibula.

It is therefore quite certain that there was no functional hyomandibula in *Macropetalichthys*, and because of the rigid shield-like covering of the head in others of the Arthrodira and in the Ostracoderma it is probable that there was also no functional hyomandibula in any of these latter fishes. In the contem-

poraneous dipnoids it was probably also wanting, for the skull of these fishes is said to be autostylic (Smith Woodward, 1891, pt II) and this precludes the presence of a functional hyomandibula.

### *WIMANIA*

*Wimania sinuosa*, a Coelacanthid from the Trias of Spitzbergen, is more primitive in several respects than the much earlier *Rhipidistia*. Its palatoquadrate is said by Stensiö (1921) to have two articulations with the neurocranium, one in the ethmoidal region and the other with a process which is said to project upward, forward and somewhat laterally from the lateral surface of the postorbital portion of the neurocranium near its dorsal margin. This process he considers to be a processus basipterygoideus, but it seems to me much more probable that it is a processus postorbitalis, that part of the palatoquadrate with which it articulates then being a processus metapterygoideus, frequently called the processus oticus or processus muscularis (Allis, 1922 *a*, 1923 *a*). The latter process is quite certainly simply an hypertrophied portion of the anterior bounding edge of the groove on the external surface of the epimandibular (palatoquadrate), and its constant connection with the postorbital process, either by articulation or by membrane, suggests that the latter process may have been developed from those branchial rays that were primarily related to the metapterygoid process. The articulation of these two processes is an archaic feature, and was doubtless acquired before a hyomandibular suspensorium was developed.

There is a short and stout epihyal, the distal end of which articulates with the ceratohyal, while its proximal end, which lies internal to the hind edge of the palatoquadrate, is directed toward the basis cranii but does not reach it by a considerable interval. Stensiö concludes that this element of the hyal arch must have been connected with the neurocranium, and suggests that it was through the intermediation of an articular cartilage, but he could find no trace of this cartilage in any of his specimens nor any trace either of a pharyngohyal or a teleostean hyomandibula.

The hyal bar of this fish had certainly acquired the Σ-shape, for this shape is always associated in recent Fishes with well developed biting jaws. There must therefore have been a pharyngohyal which articulated with the dorsal end of the epihyal and was directed postero-mesially, and both these elements of the arch lay directly internal to the lining membrane of the pharyngobranchial chamber and were not in articulation either with the otic capsule or the palatoquadrate, these being their primitive positions and relations in all Fishes. The pharyngohyal intervening between the epihyal and the otic capsule prevented the epihyal from acquiring articulation with that capsule as it does in the Selachii. The epihyal was therefore without adequate support to resist the thrust of the ceratohyal when the latter cartilage was pulled downward and backward by the ventral longitudinal muscles in connection with the opening of the mouth. This support could however readily be

acquired by utilisation of the dorsal ones of the anterior row of branchial rays of the arch to form a prefacialis cartilage similar to the prefacialis cartilage above described in early embryos of *Ceratodus*, this cartilage forming a bar extending from the otic capsule to the distal end of the pharyngohyal; and this condition had certainly been developed or was in process of development in *Wimania*. The thrust of this bar in later stages of development would tend to force the pharyngohyal away from the neurocranium, the epihyal being gradually shortened to a corresponding extent, and when the pharyngohyal had passed beyond the ventro-lateral edge of the spiracular canal it would acquire contact with the palatoquadrate, a prefacialis hyomandibular suspensorium thus being developed. The prefacialis cartilage (anterior branchial-ray bar) would then form the hyomandibula, the pharyngohyal the symplectic, and the greatly shortened epihyal the interhyal (stylohyal). The ramus mandibularis internus facialis is the ramus posttrematicus internus of the nervus facialis, and this nerve in the branchial arches always runs downward and inward across the anterior surface of the epibranchial to reach the internal surface of the arch (Allis, 1920). As the epihyal became gradually shortened this branch of the nervus facialis would shift upward along the anterior surface of the epihyal and then across the distal end of the pharyngohyal, thus acquiring a position internal to the latter cartilage, this being the relation that it has to the symplectic in all recent Fishes.

As an opercular bone developed in the ancestors of *Wimania* the posterior row of branchial rays of the hyal arch would no longer have been needed to support the gill cover, but certain of them would be in position to support and give articulation to the operculum. If the rays that were utilised for this purpose were to fuse with the chondrostean (prefacialis) hyomandibula, developed as above explained, the opercular process of that element would arise; and if cells representing others of the branchial rays were also to fuse with the hyomandibula the postfacialis part of the teleostean hyomandibula would be formed. It is quite possible that, as Edgeworth's work would seem to indicate, no definite independent element was here formed, the cells representing that element being progressively incorporated in the growing hind edge of the anterior branchial-ray bar. That an opercular process could have grown outward from the prefacialis hyomandibula as a simple process destined ultimately to give articulation to the operculum, as Edgeworth maintains, seems wholly improbable, for during the whole period of its growth it would have been non-functional. Furthermore, this process is found as a wholly independent bar of cartilage described by Budgett (1902) in a 30 mm. embryo of *Polypterus*. This bar of cartilage is said by him to project posteriorly from the convex hind edge of the hyomandibula, to be segmented into two nearly equal portions, to be postfacialis in position and to constitute the skeletal axis of the base of the external gill. The rod is said to persist in the adult as a small cartilage on the inside of the opercular bone, but this can only apply to the distal one of the two parts into which the rod is segmented, the proximal part of the rod

quite unquestionably fusing with the hyomandibula to form its opercular process.

There is thus quite certainly no functional hyomandibula in *Wimania*, and the bones on the cheek of the fish and the course and character of the latero-sensory canals are further evidence in favour of this view.

There are on the cheek of *Wimania* five dermal bones arranged in two vertical rows, the anterior row containing three bones and the posterior row two. These bones are said to be all loosely attached to the maxillary and opercular bones and the bones on the roof of the skull. The dorsal bone of the anterior row extends from the orbit somewhat more than half-way to the anterior edge of the operculum and is called by Stensiö the postorbital. Its anterior edge is traversed by the dorsal half of the postorbital portion of the infraorbital canal, the bone thus corresponding to the upper or first postorbital of *Amia*. The next ventral bone of the anterior row is a small latero-sensory ossicle traversed by the infraorbital canal. The ventral bone of the row is a long and slender bone called by Stensiö the lachrymojugal and corresponding approximately to the suborbital and lachrymal bones of *Amia*. The dorsal bone of the posterior row is the largest one of the cheek-bones and is called by Stensiö the squamoso-preopercular. Its anterior end is bounded by the small postorbital ossicle and the dorsal portion of the hind edge of the lachrymojugal, and it, together with the little postorbital ossicle, correspond approximately to the second or ventral postorbital bone of *Amia*.

A cheek-line canal enters the anterior end of the so-called squamoso-preopercular opposite the interval between the postorbital ossicle and the dorsal end of the lachrymojugal, and from there runs postero-ventrally in a curved line issuing on the ventral edge of the bone near its hind end. The ventral bone of the posterior row is a small bone called by Stensiö the preoperculo-quadratojugal. Its hind edge is traversed by the vertical cheek-line canal, and it is separated from the lachrymojugal by a space which corresponds to that occupied by the expanded hind end of the maxillary in the contemporaneous *Rhipidistia* and Chondrostei. Sewertzoff (1926) considers this to be due to reduction of the maxillary, *Wimania* being considered to be descended from the *Rhipidistia*, but it seems to me much more probable that *Wimania* represents the primitive condition, the hind end of the maxillary not having acquired the extension that it has in the other fishes. In favour of this is the fact that the maxillary is also small in *Libys polypterus* and *Macropoma mantellii*, and that Huxley says that the larger teeth in *Macropoma* are borne by the vomer and palatine, and hence belong to the primary and not to the secondary arcade.

The two bones of the posterior row on the cheek of *Wimania* are thus cheek-line bones, and all of the bones on the cheek of this fish have been developed in relation to parts of the latero-sensory system. There is no preopercular canal and no bone corresponding to the teleostean preoperculum.

The canals on the cheek of *Wimania* are thus arranged on the pattern of those on the cheek of the recent Selachii and the canals are of the selachian

type, and canals of this pattern and type are only found, in recent Fishes, either where there is no hyomandibula (Holocephali, Dipnoi) or a hyomandibula of the selachian type (Allis, 1922 *b*).

In *Libys Polypterus*, another one of the Coelacanthidae, Reis (1888) describes a hyomandibula, but Stensiö (1921) says that the bone so described is a fragment of the skull, and he also says that the hyomandibula described by Huxley in *Macropoma* is the metapterygoid process of the palatoquadrate. This latter process of *Macropoma* (hyomandibular, Huxley) is said to articulate with a process projecting dorso-laterally beneath the bones covering the roof of the skull in the postorbital region, its outer end reaching to the lateral edge of those bones (Huxley, 1866). Huxley calls this process the process *e*, and it is certainly the homologue of the postorbital process of *Wimania*. Slightly ventral to this process he describes a plate-like process *f*, which projects laterally and then ventrally and terminates with a free edge. This latter process must evidently form the dorsal and lateral walls either of a trigeminofacialis chamber such as Stensiö describes in *Wimania*, or of a jugular canal. The deep fossa said by Huxley to lie between this process *f* and the process *e* must therefore have been filled with cartilage and this cartilage probably extended a certain distance on either side of this fossa.

It is therefore probable that in these two Coelacanthids, as in *Wimania*, there was no functional hyomandibula. In his descriptions of *Macropoma*, Huxley (1866, p. 60) says: "The hyoidean arch is strong and well ossified and is connected with the hyomandibula by a very strong stylohyal." The epihyal of this fish must therefore have been similar to that in *Wimania*.

### *RHIPIDISTIA*

In these Fishes a hyomandibula and preoperculum have been developed, and the hyomandibula has sufficiently ossified to be preserved in the fossils.

In *Osteolepis macrolepidotus* and *Rhizodopsis sauroides* the hyomandibula is said respectively by Watson (1925) and Watson and Day (1916) to articulate with the outer end of a powerful process which projects laterally from the dorso-lateral portion of the otic capsule at about the middle of its length. This process is said to be in contact with the dermal bones that cover the roof of the skull, and therefore apparently does not project laterally beyond the lateral edge of the roofing bones, and as there is no corresponding projection in the edge of the latter bones those parts of the ossified portions of the chondrocranium that lie on either side of the process would seem to have been more or less covered with cartilage. This process is called by them the paroccipital, and is said by Watson to be the homologue of a similarly named process described by him in the early Amphibia and Reptilia. There is no process of the chondrocranium anterior to it, between it and the orbit, and the metapterygoid process of the palatoquadrate lies directly external to it, and was doubtless connected with it by ligaments which passed dorso-external to the articulating end of the hyomandibula. The spiracular opening lies posterior to

the process, but there is nothing to indicate the course of the spiracular canal. This process of these two fishes is thus certainly the homologue of the process *e* of Huxley's descriptions of *Macropoma*, and hence in all probability a processus postorbitalis.

The hyomandibula of *Rhizodopsis* is said by Watson and Day to be quite a large bone, perforated near its dorsal margin by a large foramen which they say is found but in few Fishes. They do not suggest that it was traversed by the ramus hyomandibularis facialis, and there is no indication of a second independent perforation traversed by that nerve, but comparison with certain specimens of *Scorpaena* (Allis, 1910, p. 43) would nevertheless seem to indicate two articulations of the hyomandibula with the cranium, and this is a distinctly teleostean character. The lower end of the bone is bent nearly at right angles and is said to form a separate piece which is attached to the palatoquadrate and is thus quite certainly a symplectic. This hyomandibulo-symplectic is therefore apparently of the teleostean type, but it is without opercular process, the operculum being supported by articulation with the preoperculum and doubtless also by ligamentous attachment of its dorso-anterior corner with the dorso-postero-lateral corner of the chondrocranium. No epihyal is described, but it must have been similar in size and shape to that in *Wimania*, its ventral end articulating with the ceratohyal and its dorsal end with the hyomandibulo-symplectic at the angle between its two portions.

The hyomandibula of *Osteolepis* resembles that of *Rhizodopsis*, but there is no perforation of the bone near its dorsal margin, and it is therefore definitely of the prefacialis (chondrostean) type.

There are in *Rhizodopsis sauroides* three infraorbital bones which correspond approximately in extent to the three bones in *Wimania*. Posterior to these bones there is a cheek-line bone and a quadratojugal as in *Wimania* but the cheek-line bone extends upward to the lateral edge of the roofing bones of the skull, there filling the space between the postorbital and preoperculum, the latter bone not being present in *Wimania*. This preoperculum is a long, curved and narrow bone extending from the spiracular opening downward to the articular end of the quadrate. The anterior corner of its dorsal end is produced into a short pointed process which forms part of the ventro-lateral boundary of the spiracular opening, and the bone is traversed its full length by a latero-sensory canal which is certainly the homologue of the preopercular canal of the Holostei and Teleostei, but there is nothing to indicate whether this canal has been developed in the selachian or in the teleostean manner, and this applies equally to this canal in the fossil Chondrostei to be later considered. The preoperculum gives articulation along its posterior edge to the operculum and suboperculum. The expanded hind end of the maxillary is interposed between the jugal and quadratojugal. No horizontal or vertical cheek-line of latero-sensory organs is described, but a horizontal line is doubtless present as it is in the closely allied *Osteolepis*.

In *Osteolepis macrolepidotus* the bones on the cheek are similar to those on

the cheek of *Rhizodopsis*, but the cheek-line bone and quadratojugal have fused to form a single bone which Goodrich (1919) calls the squamosal. Posterior to the ventral half of this bone there is a short bone which corresponds to the ventral half of the preoperculum of *Rhizodopsis*, and which Goodrich calls the preoperculum. The jugal and cheek-line bone (squamosal) of this fish are traversed by a horizontal cheek-line canal, the hind end of which lies at the level of the dorsal end of the preoperculum. The preoperculum is also traversed by a canal which is apparently continuous with a canal which extends the whole length of the mandible. That part of this canal that lies in the preoperculum is evidently the homologue of the ventral part of the preopercular canal of the recent Holostei and Teleostei, and it is probable that it continued dorsally beyond this bone in the dermal tissues along the hind edge of the cheek-line bone (squamosal). Goodrich, however, suggests that it may have been continuous with the horizontal cheek-line canal.

Watson (1925) considers the Coelacanthidae to be directly descended from *Osteolepis* but this seems improbable, for it would mean that a hyomandibular suspensorium once acquired had been gradually lost without the development of some other compensating support for the palatoquadrate; and it would seem still more improbable, if he and Watson and Day (1916) are correct in their conclusions that there are in *Osteolepis* and in *Glyptopomus* internal nasal apertures which are the homologues of those in the Stegocephalia, and hence not the homologues of those in *Ceratodus*. Stensiö says that the Coelacanthidae and *Rhipidistia* must have been descended from a common ancestor which resembles the *Rhipidistia*, but it seems to me more probable that this ancestor resembled the Coelacanthidae.

## CHONDROSTEI

In none of these Fishes, either fossil or recent, is there either a horizontal or vertical cheek-line of latero-sensory organs, so far as I can find described, but it seems certain that these lines must exist as surface organs. There is however in all these Fishes a canal line which is the homologue of the preopercular canal of the *Rhipidistia* above referred to, notwithstanding that in many of the Chondrostei the dorsal end of the canal lies anterior to the spiracle instead of posterior to it. In the recent Chondrostei I found this canal enclosed in several dermal ossicles, and I considered them to represent the preoperculum of the Teleostei (Allis, 1903, 1904). In recent Fishes this type of preopercular canal, with this dorsal end anterior to the spiracle, is always associated with a hyomandibula of the prefacialis (chondrostean) type (Allis, 1922 *b*). This does not however hold in fossil Fishes, as will be shown below.

In *Cheirolepis trailli* there are three infraorbital bones and posterior to the dorsal half of the middle one of the three there is a large bone which Watson calls (1925) the preoperculum, this bone corresponding to the cheek-line bone+ quadratojugal of *Osteolepis* and *Rhizodopsis*, but Watson describes no latero-sensory canal related to it. Along the dorso-posterior edge of this bone there

are two long and narrow bones *Y* and *X*. Bone *Y* lies antero-ventral to the spiracular opening and Watson says that appearance suggests that it was traversed by part of the horizontal cheek-line canal, but comparison with the other Chondrostei and with the *Rhipidistia* show quite certainly that both it and the bone *X* were traversed by a preopercular canal. In others of the Palaeoniscidae and in the Platysomidae and Catopteridae these two bones have apparently fused with the cheek-line bone, the canal they enclose lying close to the dorso-posterior edge of the compound bone so formed. This bone is therefore comparable to the large so-called cheek plate of *Polypterus* where a cheek-line bone has almost completely covered the preoperculum and fused completely with it, a definite line indicating its hind edge. On the cheek-line bone component of this bone of *Polypterus* there are grooves which indicate the positions of the horizontal and vertical cheek-lines of pit organs, the vertical groove lying close to the hind edge of the cheek-line bone component, and hence about directly superficial to the preopercular canal.

A hyomandibula is found in all of the Chondrostei, and in the Palaeoniscidae is, with a single exception, *Gyrolepis*, not perforated by a facialis canal (Stensiö, 1921). The hyomandibula in certain of these latter fishes has an opercular process but in others that process is wanting.

In the Platysomidae and Catopteridae the hyomandibula is said to be always perforated by a facialis canal and it apparently always has an opercular process.

In the Saurichthyidae the conditions are markedly different from those in the Chondrostei just above referred to and resemble much more those in *Rhizodopsis*.

In *Saurichthyis ornatus* Stensiö (1925 *a*) describes two infraorbital bones, called by him infraorbital 1 and infraorbital 2. These two bones are both traversed by the infraorbital latero-sensory canal and correspond topographically to the postorbital and so-called jugal bones of *Rhizodopsis*, *Osteolepis* and *Wimania*. Infraorbital 2, which is in reality a suborbital bone, forms the ventral margin of the orbit and lies internal to the dorsal edge of the shank of the maxillary. Infraorbital 1, which is a postorbital bone, forms the posterior margin of the orbit and extends upward from the dorsal edge of the hind end of the suborbital to the lateral edge of the dermo-sphenotic. Its hind edge articulates with the anterior edge of a bone called by Stensiö the suborbital or bone *Px*. This latter bone has the shape of a parallelogram, its dorsal edge articulating with the lateral edge of the bones on the roof of the skull, its hind edge forming the ventral portion of the anterior boundary of the spiracular opening, its ventral edge being overlapped externally by the dorsal edge of the expanded posterior portion of the maxillary, and its anterior edge articulating with the postorbital. The antero-ventral corner of the bone touches the hind edge of the suborbital and cuts the postorbital bone off from all contact with the expanded hind end of the maxillary. This bone *Px* has exactly the position of the antero-dorsal corner of the so-called squamosal of *Rhizodopsis*, and I

consider it to be the homologue of that part of that bone, the remainder having been suppressed by the gradual and progressive overlapping of the greatly expanded posterior portion of the maxillary. This little bone of *Saurichthyis* is therefore a persisting portion of what I have called the cheek-line bone of the *Rhipidistia*.

Posterior to the ventral half of the hind end of the maxillary there is a small bone which represents the quadratojugal of *Rhizodopsis* and the posterior ventral corner of the squamosal of *Osteolepis*, this bone thus being wholly separated from the persisting remnant of the cheek-line bone by the expanded hind end of the maxillary.

The spiracular opening lies approximately opposite a line that would cut off the anterior third of a bone called by Stensiö the intertemporo-supratemporo-extrascapular. The intertemporal and supratemporal portions of this latter bone correspond to what is usually called by English authors the dermopterotic. The extrascapular part of the bone corresponds to what is called by English authors the supratemporal and by German authors the extrascapular, but is called by Watson and Watson and Day in recent publications, the tabular. To prevent confusion I shall hereafter employ the term used by Stensiö. The posterior edge of the spiracular opening is formed by the anterior edge of a bone called by Stensiö the preoperculum, the ventral edge of the opening being bounded by a small process of this bone which projects anteriorly from the ventral end of its anterior edge.

The preoperculum, above referred to, has a long straight dorsal edge which lies in a horizontal position, separated from the lateral edge of the bones on the roof of the skull by a certain space, this space apparently having been occupied by an anterior extension of the dorsal end of the hyobranchial cleft. The anterior edge of the bone is short, lies at right angles to its dorsal edge and forms the posterior boundary of the spiracular opening. From its ventral end a short process extends forward and forms part of the ventral boundary of the spiracular opening. The hind edge of the bone is long and straight, it lies at right angles to the dorsal edge and gives articulation throughout its entire length to the operculum. The ventral edge of the bone is long and concave, the concavity directed antero-ventrally, and the edge of the bone is here overlapped externally throughout its entire length by the expanded hind edge of the maxillary. The bone has the appearance of being formed by two lamellae, a superficial and a deeper one, the two lamellae being everywhere fused with each other except at about the middle of the length of the bone, where they are separated from each other, except at their extreme dorsal edges, by a large pocket which extends upward in the bone from its ventral to its dorsal edge, where it ends with a rounded edge. The external and internal lamellae of the bone run directly into each other, this giving the appearance of the external lamella having been bent inward and downward upon itself to form the internal lamella, and Stensiö so describes it. A latero-sensory canal, which is certainly the homologue of the teleostean preopercular canal, enters the bone

on its dorsal edge at about its posterior third, considerably posterior to the spiracular opening, runs postero-ventrally and then ventrally along the hind edge of the bone and issues at its postero-ventral corner. Beyond this point the canal lies in the dermis posterior to the quadratojugal, between it and the operculum.

The preoperculum of this fish is thus certainly of the teleostean type and the homologue of the preoperculum of *Rhizodopsis*, the little process that projects forward to form the ventral boundary of the spiracular opening corresponding to the process in *Rhizodopsis* which projects antero-dorsally from the dorsal end of the bone in the same relation to the spiracular opening. The spiracular opening in *Saurichthyis* has simply shifted relatively much farther forward than in *Rhizodopsis*, and the dorsal end of the preoperculum has expanded correspondingly to occupy the space thus left vacant. Stensiö considers this bone to be the homologue of the preoperculum of the Palaeoniscidae, Platysomidae and Catopteridae, and hence the homologue of the squamosal of Watson and Day's descriptions of *Osteolepis* and of his own descriptions of *Wimania*. This is however in my opinion an error, for the latter bones always contain a cheek-line component which forms no part of the bone in *Saurichthyis*.

The palatoquadrate is said to have anterior horizontal and posterior vertical portions, the dorsal end of the latter portion fitting into the little pocket in the ventral edge of the preoperculum, above described, its dorsal end being bent outward and downward in a curved line and fitting closely against the curved dorsal wall of the pocket. This part of the palatoquadrate is evidently a metapterygoid process. Ventral to this process the hind edge of the bone extends vertically to the articular end of the quadrate and articulates throughout its entire length with the internal surface of the preoperculum. On the internal surface of this part of the bone there is a rounded groove which lodges the symplectic portion of the hyomandibulo-symplectic, as will be explained immediately below. The ventral edge of the maxillary has fused with the lateral edge of the horizontal plate of the palatoquadrate. The maxillary, preoperculum and palatoquadrate are thus firmly bound together and enclose within them a space which gives insertion to the musculus adductor mandibulae, that muscle passing downward through a large fenestra in the hind end of the horizontal plate of the palatoquadrate to reach and enter the mandible. The preoperculum and maxillary thus in a measure support and suspend the palatoquadrate, but as they themselves are simply suspended in the dermis they do not form an effective suspensorium.

A hyomandibula is not described by Stensiö in this fish, but is in *Saurichthyis hamiltoni*. This so-called hyomandibula of the latter fish is a long and slender rod without opercular process, and its dorsal end is said to articulate with the posterior field of the labyrinth. The dorsal half of the bone is thicker and broader than the ventral half and it lies in a nearly horizontal position. The ventral half of the bone arises from the ventro-anterior portion of the distal end of the dorsal half, projects postero-ventro-laterally at an obtuse angle

to the upper half, and lies in the groove above referred to on the postero-mesial surface of the hind end of the palatoquadrate, its ventral end reaching to the level of the articular end of the quadrate and lying mesial to it.

The two parts of this so-called hyomandibula thus have to each other and to the palatoquadrate exactly the relations of the hyomandibula and the symplectic of the recent Holostei and Teleostei, and I shall so hereafter refer to them. On the antero-lateral surface of the symplectic, beginning near its dorsal end, a groove runs downward to the ventral end of the bone, and Stensiö concludes that this groove must have lodged the ramus mandibularis facialis, the external and internal branches of the nerve separating from each other after the nerve reached the ventral end of the symplectic. He therefore considers the relations of the ramus hyomandibularis facialis of this fish to his so-called hyomandibula to have been similar to those in *Polypterus*. This would be correct if this bone was simply a hyomandibula, but could not be if its ventral half is a symplectic as I conclude, for the rami mandibularis internus and externus facialis always run downward on opposite sides of the latter bone in all recent Fishes. It therefore seems to me probable that the groove in question was traversed by the dorsal portion of the so-called arteria hyoidea of recent Fishes, this artery always passing external to the symplectic on its way upward to reach the pseudobranch.

The ceratohyal of *Saurichthyis ornatus* is said to be a long and slender bone, the middle portion of which is ossified. There is no separate ossification at the proximal end of the bone as there is in the recent Holostei and Teleostei. Stensiö does not give any indication as to how this bone articulated with the hyomandibulo-symplectic, but comparison with recent Fishes and with *Wimania* would indicate that there must have been a short epihyal (interhyal, stylohyal) connecting it with the hyomandibulo-symplectic at the angle between the two parts of the bone. Stensiö however found no indication of this element.

## CONCLUSIONS

In the early ancestors of the gnathostome Fishes the cartilaginous bars of the visceral arches lay directly internal to the lining membrane of the pharyngobranchial chamber, each arch lying in a single plane. The dorsal end of each bar was directed toward the ventro-lateral surface or ventro-lateral edge of the central axial skeleton and connected with it by more or less developed connective or ligamentous tissue. Later, as the mouth parts developed, the bars of all the more anterior arches acquired the Σ-shape, the four limbs of the Σ being formed, from above downwards, by the pharyngeal, epal, ceratal and hypal elements of each bar. The dorsal end of each bar, now formed by the dorsal end of the pharyngeal element, was still directed toward the ventro-lateral edge of the central axial skeleton and connected with it by connective or ligamentous tissue, the line of attachment lying ventral to the vena jugularis between it and the dorsal aorta. The otic capsule of either side lay approximately between the dorsal ends of the hyal and mandibular bars, and as it

developed it pushed those ends somewhat apart and approached the articulating ends of the pharyngeal and epal elements of the hyal arch, the ventral (distal) end of the pharyngohyal articulating with the dorsal (proximal) end of the epihyal and lying between that end of that element and the lateral wall of the capsule. These relations of these elements of the hyal arch to each other, to the lining membrane of the pharyngo-branchial chamber, to the otic capsule and to the palatoquadrate were common to the ancestors both of the Elasmobranchii and the Osteichthyis, and may be called the presuspensorial condition.

In certain of these presuspensorial Elasmobranchii the dorsal end of the pharyngohyal acquired articulation with the lateral surface of the otic capsule, its ventral end acquiring contact with the palatoquadrate, thus giving origin to the hyomandibula of the Batoidei. In certain others of these fishes the pharyngohyal was withdrawn from its articulation with the dorsal end of the epihyal, and that end being exposed acquired articulation with the lateral surface of the otic capsule, thus giving rise to the hyomandibula of the Selachii. In both instances the surface of articulation with the otic capsule naturally lay ventral to the vena jugularis, between that vein and the lateral dorsal aorta, for this was the region of attachment of the connective or ligamentous tissues that primarily connected the dorsal end of the hyal bar with the central axial skeleton, and this articulation of the hyomandibula ventral to the vena jugularis is not known in any other fishes either recent or fossil. In certain others of the Elasmobranchii the dorso-mesial edge of the palatoquadrate fused with the neurocranium, thus giving origin to an autostylic suspensorium, the pharyngeal and epal elements of the hyal arch retaining their presuspensorial relations to each other and to adjacent structures (Holocephali).

The support thus given to the jaws by each of these three types of suspensorium greatly increased their biting capacity, and this gave to these early Elasmobranchii, and specially to the Selachii, a marked advantage over other fishes that had not acquired such support of the jaws. Certain of these other fishes therefore acquired a protective covering of dense dermal bone, the dorsal surface of the head and cheeks being covered by a rigid shield-like plate (Ostracoderma, Arthrodira). This rigid covering of the cheek was unfavourable to the development of a hyomandibular suspensorium, for it permitted but little, if any, of that outward and inward movement of the cheeks that is characteristic of the proper functioning of a hyomandibular suspension of the jaws. The conditions were not however unfavourable to the development of an autostylic suspensorium, and this was developed in certain of these fishes (Dipnoi), the pharyngohyal and epihyal retaining their presuspensorial relations to each other as they do in the Holocephali, but the pharyngohyal in the recent *Ceratodus* fuses with the ventral surface of the otic capsule and with the hind edge of the palatoquadrate.

In certain others of these early Osteichthyes the bones covering the cheek were independent of each other and in movable articulation with the bones on the dorsal surface of the skull. The pharyngohyal and epihyal of these fishes

at first retained their presuspensorial relations, this condition being shown in *Wimania*, a Crossopterygian of the family Coelacanthidae. The pharyngohyal still here retained its articular relation with the dorsal end of the epihyal, lying between that element and the lateral surface of the otic capsule. This prevented the development of a selachian hyomandibula, and this type of hyomandibula, articulating with the otic capsule ventral to the vena jugularis, is not known in any of these fishes either recent or fossil. The conditions here were however favourable to the development of a different type of hyomandibula.

The branchiae and related branchial rays on the anterior surface of the hyal arch became reduced or aborted as the spiracular cleft became reduced, but certain of the dorsal rays persisted in protective relation to the vena jugularis, forming an anterior branchial-ray bar, the dorsal end of which articulated with the otic capsule dorsal to that vein, while its ventral end either articulated with or fused with the distal end of the pharyngohyal. This then gave rise to a prefacialis but non-functional hyomandibula, and is represented in early embryonic stages of *Ceratodus* and probably also in the fossil Coelacanthidae. The distal end of the pharyngohyal then acquired articulation with the palato-quadrate, passing latero-ventral to the reduced spiracular cleft and, becoming a symplectic, converted the non-functional prefacialis hyomandibula into a functional one; the symplectic remaining independent of the hyomandibula in certain Fishes as typically represented in the recent Chondrostei, but fusing with the hyomandibula in other Fishes as typically represented in the fossil Saurichthyidae.

This simple prefacialis hyomandibula then underwent modification. In certain Fishes certain of the posterior branchial rays of the hyal arch acquired articulation with the operculum by their distal ends while their proximal ends fused with the prefacialis hyomandibula. This gave origin to an opercular process and a simple prefacialis hyomandibula with this process is found in certain of the Palaeoniscidae.

In certain other Fishes, material derived from other branchial rays of the posterior row fused with the prefacialis hyomandibula and so gave origin to the teleostean type, this being found fully developed in the recent Holostei and Teleostei, and apparently in process of formation in the Platysomidae and Catopteridae.

In *Rhizodopsis* the hyomandibula is apparently of the teleostean type but without opercular process. In the recent *Polypterus* the hyomandibula is a prefacialis one with opercular process, that part of the postfacialis component of the element that lies dorsal to its opercular process apparently being represented in the adult by ligaments, but Edgeworth found no trace of this ligament in his 75 mm. specimen, and Budgett does not describe it in his 30 mm. specimen.

The conditions in these fossil fishes thus favour my contention that the selachian hyomandibula is an epihyal, and that the teleostean hyomandibula was not derived from it by the simple shifting upward of its surface of articula-

tion with the otic capsule from a position ventral to the vena jugularis to one dorsal to that vein. The conditions do not, however, favour my assumption that a definite postfacialis branchial-ray bar was ever developed, but they definitely favour the assumption that this part of the hyomandibula, and specially the processus opercularis, was developed from material derived from the posterior row of branchial rays.

PALAIS DE CARNOLES,
MENTON, FRANCE.
*February* 1, 1927.

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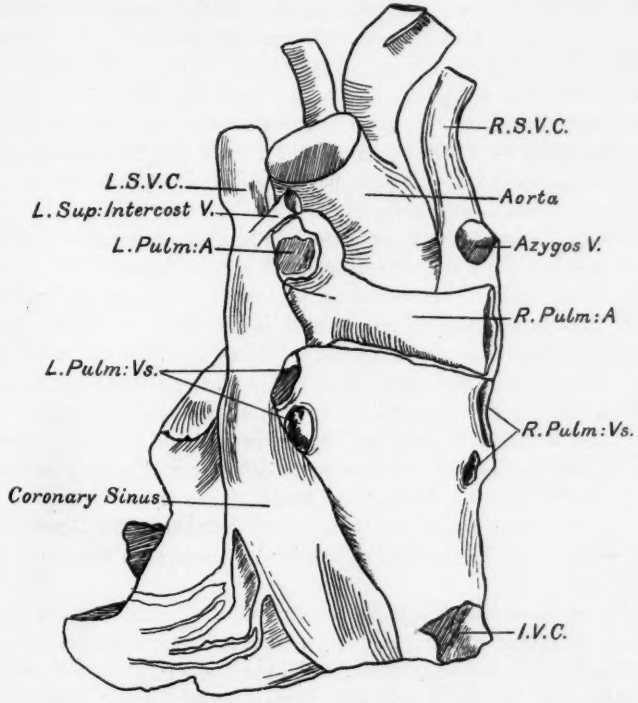
# A CASE OF BILATERAL SUPERIOR VENAE CAVAE IN THE ADULT

By P. N. B. ODGERS, M.Ch., F.R.C.S.
*Department of Human Anatomy, Oxford University*

This specimen of bilateral superior venae cavae was obtained in the University dissecting room from a male subject, aged 68. As in other recorded cases, the persistent left cava crossed the aortic arch and the root of the left lung, to continue as a large coronary sinus and open into the right atrium.




There was no cross branch—no transverse jugular vein—in this case: the only veins that opened into the left cava being the left superior intercostal and the left inferior thyroid veins. The arrangement of the azygos veins was normal, all draining into the right side. The Eustachian valve was very poorly developed, while the valve of the coronary sinus (Thebesii) was absent. No other abnormalities of the heart or great vessels were present.

Whilst this condition does not appear to be uncommon in foetuses and young children, in which it is often accompanied by other gross abnormalities incompatible with life, only a minority of cases have been found in adults.

In 1916 McCotter (1) found 120 cases reported in all, of which only 36 were classified by him as indubitably having occurred in adults. To these must be added the 3 cases he observed himself and 8 more in the literature since that date, reported respectively by Baroni (2), D. C. and H. C. Keyes (3), Donadio (4), Sokolov (5), J. H. Smith (6), A. Gibson (7), Huffmire and Bower (8), and Le Count (9) giving, with the instance now recorded, a total of 48.

I have been unable to obtain the papers of Baroni (2) and Sokolov (5), while two of the remainder differ so much from the others that they should hardly perhaps be included. In one of these latter, A. Gibson (7) found simply a pervious venous channel passing from the left superior intercostal vein down to the left extremity of the coronary sinus; otherwise the venous arrangement was normal. In J. H. Smith's (6) case, the coronary sinus did not open into the right atrium at all but the cardiac veins united to form a vein which passed up in front of the root of the left lung to open into the left superior intercostal vein, which itself joined the left innominate vein. In this connection, Le Cat's (10) case may be recalled. In a child 8 days old, "les veines coronaires reunies dans un seul tronc qui, sans pénétrer dans l'Oreillette droite, se jetait dans la veine souclavière gauche."

With these 4 cases omitted there are details of 44. A point of some interest in these cases is the presence or absence of a cross branch between the two superior cavae. Out of these 44 there was no such connection in 21, a small one in 13, while in 10 a normal anastomosis is described. In slightly more than half the cases then, there is a cross branch found and this fact would seem to make Gegenbauer's original hypothesis—that the persistence of the left cava depends on the non-development of such an anastomosis—invalid.

Ancel and Villemin (11) point out, however, that the efficacy of this branch must vary with its obliquity and suggest that four grades may be imagined:

(*a*) No cross branch is formed and two equal cavae persist.

(*b*) The anastomosis is present but so horizontal that it will not deflect the blood current in the left primitive jugular vein and so a well-developed left cava persists.

(*c*) The anastomotic vein is not so horizontal as in (*b*) and yet not so vertical as the primitive jugular: a much smaller left superior cava will result.

(*d*) Finally, if the anastomosis is oblique from right to left rather than from left to right, the right cava will disappear and the left alone survive.

I must thank Prof. Arthur Thomson for kindly allowing me to publish this case.

## ADDENDUM

Since the above note was written, Hurley and Coates (12) have published a case of bilateral superior venae cavae in which the veins were "united together by a fibrous band representing the remains of the left innominate vein." The subject was a female, aged 53.

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# HERNIA THROUGH THE CENTRAL TENDON OF THE DIAPHRAGM (CAT)

By GRACE BRISCOE, M.B., B.S.

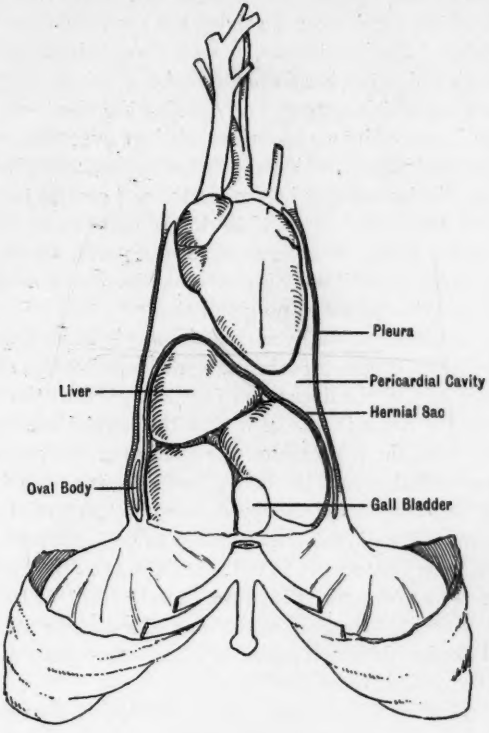
The cat was used for an experiment on the diaphragm. It was large, well grown and appeared healthy. It drank about 100 mg. of chloralose in milk, and took ether quite normally. The heart was beating well and respiration appeared to be normal.

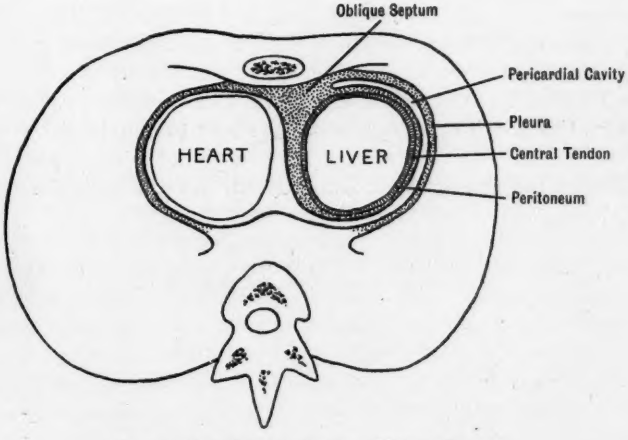
On opening the abdomen it was noticed that the abdominal muscles were extremely tense, so much so that it was quite difficult to get a view of the under surface of the diaphragm. The central incision had to be enlarged, and then it was seen that the diaphragm was not normal. At first sight the median raphe could not be seen; the left side of the diaphragm appeared to be more extensive than the right side, and it was then seen that the median raphe was pulled over to the right. A mass of omentum and stomach appeared to fill the right dome, and to protrude up through the diaphragm into the chest.

On pulling down the stomach and withdrawing about three inches of omentum from the opening in the diaphragm it could be seen that the liver was much distorted, and one lobe passed up through the orifice into the chest. The whole organ was lying more posteriorly than usual, and was mostly hidden by the stomach and omentum. The end of the omentum and the portion of curvature of the stomach close to the orifice were stained with bile. A finger passed through the hernial opening appeared to come directly on the beating heart inside the chest.

The chest being opened, and the sternum cut away, it was noticed that the under surface of the sternum was stained with bile. The chest was much elongated, and there was a large tubular sac lying in the mid-line, more to the right than the left. This tubular sac was in the shape of a blunt cone, and was 40 mm. in diameter at the base. The base filled the space usually occupied by the central tendon, and the cone extended upwards for 75 mm. The upper part was obviously occupied by the heart, which was lying more obliquely than usual. The apex of the heart was 30 mm. above the level of the diaphragm. The lower part of the cone was occupied by firm lobular bodies. The outer covering of the sac was pleura, and was continuous everywhere with the parietal pleura.

On making an opening into the sac, it was found that the heart was shut off from the hernial cavity by the pericardium. The pericardial sac was discrete and invaginated by the hernial sac in such a way that there were large prolongations of the main pericardial sac posteriorly and laterally, and these recesses reached down to the level of the diaphragm. Anteriorly there was an oblique septum




Cross section showing Anterior Oblique Septum.

following the line of the right border of the heart, which was common to the pericardial sac and the hernial sac. In short, the much enlarged pericardial sac completely enveloped the hernial sac, except along this oblique septum, and the orifice through which the hernia protruded.

The tubular mass which appeared on opening the chest was therefore provided below the heart with two coverings distinct everywhere, except along the oblique septum already mentioned. The outer layer was formed by pleura and pericardium, the inner layer by pericardium, ? central tendon, and peritoneum. Between these two layers, close to the diaphragm on the right side, was a small flattened body, movable, except at one point. It was about 10 mm. in diameter. The nature of this body is doubtful. Section showed fibrous tissue, a few unstriped muscle fibres and no gland tissue.

Inside the true hernial sac was liver, considerably lobulated, the gall bladder, and about three inches of greater omentum. The gall bladder came up against the sternum. Posteriorly the liver was firmly attached to the sac. When the omentum was pulled down it was seen that the hernial sac was open to the peritoneal cavity, and the peritoneum was continuous everywhere.

From the abdominal aspect the hernial orifice was sharply defined, about 25 mm. in diameter. It occupied the space usually taken by the central tendon. The muscular part of the diaphragm appeared to be fairly normal except that the muscle fibres were very scanty in the anterior part. The crura were normal.

The whole chest was elongated 130 mm. from the first rib to the apex of the subcostal angle, instead of the normal 100 mm. The number of ribs was normal (13 pairs). The left phrenic was 170 mm. in length from upper root to insertion, but otherwise it appeared to be normal.

Hernia through the central tendon of the diaphragm appears to be an uncommon condition. Sir Arthur Keith[1] found three cases in a collection of 34 museum specimens of human diaphragms. A specimen from a Belgian hare somewhat resembling this hernia was described by Prof. A. Thomson[2]. An accessory organ was found in the chest, thought at first to be an extra heart, until section showed it was liver tissue. There was a sinus-like dilatation of the central tendon in front of the vena cava. The accessory organ was continuous with this pouch by a circular orifice about 10 mm. in diameter.

My thanks are due to Prof. Lucas Keene for the assistance she has given me.

[1] *B.M.J.* 29 October, 1910.
[2] *Journ. Anat. and Phys.*, vol. xxxv, p. 16.

# CARDIAC MALFORMATION WITH VASCULAR ANOMALIES[1]

By ALEXANDER BLACKHALL-MORISON, M.D., F.R.C.P.

The developmental relation of the vascular system to the heart is a subject of both scientific and clinical interest. That there is a harmonious constancy in their relation to one another in the normal development of both heart and vessels is a matter of common experience. But the congenitally malformed heart is frequently associated with anomaly in the development of the related vascular system. Whether cardiac and vascular anomalies are entirely independent of one another in their genesis, or whether abnormality in one provokes abnormality or abnormal adaptation in the other is likewise a question provocative of thought. Or, again, whether both conditions are attributable to a common cause is also a matter of interesting speculation.

That obstacle at a certain point and at a certain stage of cardiac development involves diversion of the circulation in its impulse, career or design towards the attainment of its purpose is manifest. That such diversion is associated with morphological deviation from the average normal in cardio-vascular growth is likewise unquestionable. These points, which are not only of academic or theoretical but also of clinical or practical interest, may best be considered by the study of a concrete or specific instance of congenital cardio-vascular error in development, of a type which constitutes a large proportion of all cardiac malformations which come under the notice of the physician. Sir Arthur Keith places this percentage as high as ninety-six in his Schorstein Lecture (*Lancet*, 20 December, 1924).

W. H. T., aged 16 months, one of six children of healthy parents, whose five brothers and sisters were also healthy, was admitted under my care into the Great Northern Central (now the Royal Northern) Hospital on 16 April, 1914, with his nose, lips, hands and feet cyanosed, and a regular but feeble pulse. The area of cardiac dullness was considerably increased, there was precordial bulging to the left of the sternum, dullness on percussion to the right of it, a loud systolic bruit was heard over the praecordia generally, but loudest at the level of the nipple; it was also heard, but faintly, in both paravertebral grooves and more loudly on the left; the pulmonary signs were normal, yet the child was cyanosed especially when crying, and had clubbing of the fingers and toes; there was no palpable thrill in the praecordia.

A note made on 30 April states that when the child was lying peacefully in bed there was no cyanosis, that the physical signs were as previously noted, and that the systolic bruit, loudly heard in the situation indicated, was only

[1] A paper read at the International Anatomical Conference in April 1927.

faintly audible in the arteries of the neck and not at all in the abdominal aorta or down the spine. It was therefore concluded that the lesion producing the murmur was probably due to a defect in the ventricular septum. The child became febrile on 2 May, showed signs of congestion at the base of the right lung, and died on 5 May, 1914.

The general necropsy was made by the pathologist to the Hospital (Dr E. H. Shaw) on 6 May, when the pleurae, lungs, pericardium and abdominal organs were found to be normal, the latter merely showing passive congestion. I subsequently examined the heart and attached blood vessels myself, with the following results:

*Heart.* Enlarged and most so in its right chamber, the right atrium capacious and with well-developed pectinae and trabeculae, a foramen ovale pervious indeed, but closed almost completely by a membranous curtain, the coronary sinus normal, as also the superior and inferior caval entrances.

The right ventricle is hypertrophied, its walls at their thickest measuring 6–7 mm. and their papillary muscles large and powerfully developed. The exterior of the right ventricle measures 6 cm. longitudinally and 4 cm. transversely.

The anterior and posterior cusps of the tricuspid valve are well developed, and the posterior has attached to it a number of nodules resembling hardened granulations, two of these are also attached to one of the tendons of the anterior cusps. This raises the question whether these indicate a foetal endocarditis. I am inclined to think that they do not. The internal cusp of this valve is attached to the posterior segment of a patent inter-ventricular communication of considerable size at the upper boundary of the septum. The aorta opens into the right ventricle. The infundibulum appears to be entirely absent, and the trunk of the pulmonary artery is diminutive and lies to the right of the aorta. Its orifice is quite occluded, the site of its valves being occupied by a membranous cul-de-sac which leaves little or no indication of individual valve cusps. Both right and left main branches of the pulmonary artery are well developed.

The left atrium is much smaller than the right, the posterior and aortic cusps of the mitral valve well developed, and the entrances of the pulmonary veins, two in number, are normal.

The left ventricle measures externally 4 by 4 cm. and the walls at their thickest 5 mm. The aorta opens into the left as it does into the right ventricle but more directly into the latter. The three cusps of the aortic valve are normal, as are the two coronary arteries. The arch of the aorta passes to the right and backwards over the root of the right lung, and its descending portion lies to the right of the oesophagus. The right subclavian and common carotid arteries arise separately, and the left carotid, subclavian artery and the ductus arteriosus from a common or innominate trunk, which springs from the ascending arch of the aorta. The ductus arteriosus is pervious and opens into the diminutive trunk of the pulmonary artery.

In this case it will be observed that the main aortic arch springs from the right instead of the left fourth visceral arch, gives off the right common carotid and subclavian arteries separately, as the aortic arch usually does the vessels

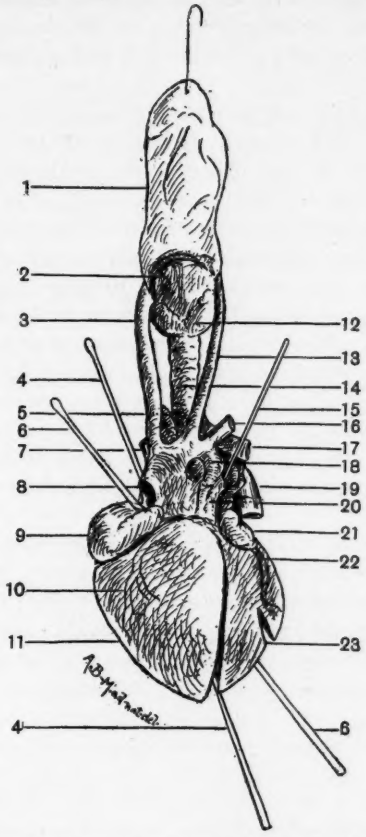



Fig. 1. 1, tongue; 2, larynx; 3, right carotid artery; 4, probe passed through the right ventricle into the aorta; 5, arch of the aorta passing to the right; 6, probe passed through the left ventricle into the aorta; 7, right subclavian artery; 8, opening into the base of the aorta; 9, the right auricle; 10, a branch of the right coronary artery; 11, right ventricle; 12, stump of the thyroid gland; 13, left carotid artery stretched by pendency and twist of the suspended heart; 14, trachea; 15, probe passed from above into the diminutive and atresic pulmonary artery; 16, left subclavian artery; 17, left bronchus; 18, ductus arteriosus; 19, oesophagus; 20, diminutive pulmonary artery; 21, left auricle; 22, branch of left coronary artery; 23, left ventricle.

on the left when it springs from the left fourth visceral arch, while the transposed arrangement in this case shows an innominate stem springing from the left fourth arch which gives off not only the left common carotid and subclavian arteries, but also the ductus arteriosus, while the pulmonary stem, robbed of

its companion ductus arteriosus, in its origin from the left sixth visceral arch, is diminutive at its commencement, without connection with the cardiac ventricle, and functionless. Yet, notwithstanding, its pulmonary branches are well developed, and, through the ductus arteriosus, conveyed sufficient blood to the pulmonary circuit for delivery to the left auricle, leaving the circulation in the lungs normal, as both physical signs and post-mortem examination proved.

The question then arises whether the hypoplastic development of the pulmonary artery at its commencement arose from failure in development from the sixth left arch, that is, from above, or whether it was due to obliteration of the infundibulum, that is, from below.

I have already referred to Sir Arthur Keith's work on the fate of the bulbus in the human heart, a subject which had exercised his thoughts many years before he published his Schorstein Lecture of 1924 (*loc. cit.*). His original views on the subject were published in the *Proceedings of the Anatomical Society of Great Britain and Ireland* in 1905. He attributes the anomalies in question to the failure of the infundibulum in the right ventricle to expand and become harmoniously incorporated with the lower section of the chamber. Contracting sometimes to a mere chink, and closing the exit by way of the pulmonary artery and ductus arteriosus to the systemic aorta, it leaves blood to find its way through the foramen ovale and imperfect ventricular septum into the left heart.

Does, however, such infundibular stricture account for the anomalous situation of the aorta when it arises from both ventricles, and for the anomalous origin of trunks and branches from its arch. Manifestly I think it does not, and we know that the pulmonary artery and the aorta may be transposed even when the septum ventriculorum is perfect, and that the numerous vagaries in the transformation of the visceral arches producing blood vessels may, apparently, bear no relation to intracardiac conditions.

On the other hand, the heart embryologically exists prior either to blood transportation or to vessels leading to it or issuing from it, and arrests of development within it may be reasonably regarded as possibly having no relation to its vascular inlets and outlets at some period of its development. Nevertheless, at a certain stage the influence of intracardiac conditions on the vascular system, and of the latter on intracardiac states, seems admissible.

Dr T. B. Peacock's work on cardiac malformations (London, 2nd ed. 1866) is still the best and most interesting treatise in this country on the clinical history and anatomical features of cardiac malformation, and his general conclusions, from his study of the considerable number of cases he investigated personally and in the literature of the subject, agree with those of others who have studied the matter. They may be expressed in the following formulae which I may term mnemonic, although they also contain, in my opinion, morphological truth and are applicable to the majority of such cases as that which I have related as representative of a large class. In these formulae the minus

sign indicates deficiency or diminution, the plus sign presence or increase, × normality, and ? uncertainty.

(1) (P. A. −) + (S. V. −) = (R. A. and R. V. +) + (L. A. and L. V. −) + (Ao. +) + (F. O. −) + (D. A. +).

(2) (P. A. −) + (S. V. +) = (R. A. and R. V. −) + (L. A. and L. V. +) + (Ao. ×) + (F. O. +) + (D. A. ?).

That is, when the pulmonary artery is atresic or hypoplastic and the septum ventriculorum is imperfect, the right auricle and ventricle will be found enlarged, and the left auricle and ventricle diminished in size, the aorta usually large, the foramen ovale closed or nearly so, and the ductus arteriosus usually, but not always, permeable.

On the other hand, when the pulmonary artery is atresic or hypoplastic, and the septum ventriculorum complete or perfect, the right auricle and ventricle will be found to be reduced in size, the left auricle and ventricle more or less capacious, the aorta probably normal, the foramen ovale open or large, and the ductus arteriosus less certainly permeable than in the former category.

We may, therefore, I think, reasonably conclude that the heart and blood vessels have an independence in developmental anomaly, but, nevertheless, at a certain stage in cardio-vascular growth, when the circulation of the blood is established, that they mutually influence their respective anatomical states.

On one other point in the fate of the bulbus I should like to remark. The tissue at the base of the aortic cusp of the mitral valve is regarded by embryologists (Keith, *loc. cit.* p. 1271) as "all that is left of the lesser curvature of the bulbo-ventricular tube of the foetal heart, in the left ventricle." This remnant, if it be such, is, however, a portion of the auricular sphincter of the mitral orifice, and may be shown to be in anatomical continuity with the atrial muscle, and quite unconnected with the ventricular muscle at the ventricular portion of the atrio-ventricular orifice; that is, it appears to have coalesced with auricular muscle entering the valve segment from above.

# COXA VARA DUE TO CONGENITAL DEFECT OF THE NECK OF THE FEMUR

By H. A. T. FAIRBANK, D.S.O., M.S., etc.

The condition of the femur described in this paper is usually called cervical or infantile coxa vara. Coxa vara is said to exist when the angle of inclination of the femur is below normal limits, say, below 125°. The particular type of coxa vara dealt with here is associated with characteristic anatomical peculiarities. Before describing the anatomy it would be well, perhaps, to refer briefly to the chief clinical features of this type of case. The onset is usually insidious and the history somewhat vague, but in many the limp, which always accompanies the deformity, is said to date from the time the child began to walk. Both sexes are affected without any great preponderance in either. In at least a third of the cases the condition is bilateral. Occasionally this type is seen on one side and a simple coxa vara on the other. There is a marked limp and in the bilateral cases a waddling gait not unlike that so commonly seen in congenital dislocation of the hip joints. The children complain of stiffness after rest, and pain after walking, in fact many, more particularly those with bilateral deformity, are severely crippled. Some of the cases are well below the average in height. On examination the chief features seen are raising of the trochanter, with, of course, shortening of the limb, marked limitation of abduction, and to some extent of rotation. The hip is usually flexed, extension being limited or obliterated, and there is marked increase of the normal lumbar spinal curve, i.e. lordosis. The age at which the cases commonly come before the surgeon is 6 to 8 years, but, as already stated, symptoms commonly date from much earlier. As can be readily understood from the radiographic appearances, there is a strong tendency to increase of the deformity, but this does not invariably occur. The worst cases of coxa vara met with in adult life, apart from fractures, are the result of this affection.

Our knowledge of the anatomy of these cases is almost entirely gleaned from the study of the radiographic appearances, which vary considerably with the age of the patient and the degree of the deformity. The fundamental anatomical abnormalities are best seen in the younger children with deformity of moderate degree. All the essential features are seen in fig. 1, which shows the hips of a boy aged 6½ years with bilateral coxa vara. Briefly the following are the changes seen in both hips:

1. The angle of inclination is reduced to something below a right angle.

2. The head of the femur is unusually translucent, is situated rather low in the acetabulum, and seems to be abnormally thick or deep, as if the ossific

Fig. 1. Bilateral infantile or cervical coxa vara, showing triangular portion of neck ossifying by separate centre. (Boy aged 6½ years.)

Fig. 2. Unilateral infantile coxa vara showing triangular fragment partially fused to neck. (Aged 10 years.)

centre were extending into the neck and displacing outwards the epiphyseal line. This is more obvious above than below.

3. There is a fragment of bone, roughly triangular in shape, occupying the lower part of the neck. This fragment, the density of which approximates to that of the rest of the bone rather than to that of the head, is bounded by two clear bands traversing the neck, and forming together an inverted V. The inner of the two limbs of this V is undoubtedly the epiphyseal line, while the outer is quite abnormal, and its presence constitutes, with the triangular fragment, the characteristic feature of this type of coxa vara.

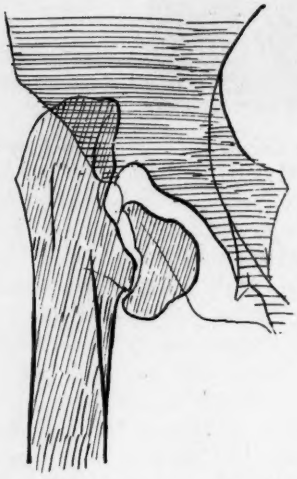


Fig. 3. Infantile coxa vara, later stage, showing greatly depressed head and short neck.

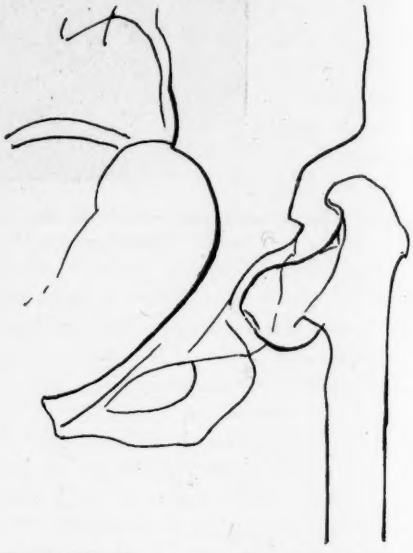


Fig. 4. Infantile coxa vara, later stage, showing neck fairly well formed but greatly depressed.

Now what is the fate of this fragment of bone? If the deformity progresses the fragment retains its relation to the head and descends with the latter. In older children it is more difficult, and it may be impossible, to distinguish this piece of bone. It has been recognised in one hip as late as 8 years, and in both femora at 10 years. It may fuse with the neck and then appears as a lip projecting nearly vertically downwards (fig. 2). The neck seems to be striving to retain some connection with the grossly depressed head. On the other hand the abnormal clear band in the neck may remain, in which case presumably the fragment fuses with the head. The later stages of the deformity reveal two distinct conditions. In one the neck is poorly formed and seems almost non-existent, while the head lies so low that it is opposite the shaft rather than the trochanteric region of the bone (fig. 3). In the other

there is a neck of good length, but this is inclined downwards to reach the head, and forms an acute angle with the line of the shaft (fig. 4). The pathological evidence of the nature of the condition is very meagre, Elmslie only being able to find four specimens, all obtained from adults with gross deformity. There was a narrow fibrous intersection present in the neck of the femur. In children the abnormal clear line in the neck is presumably occupied by unossified cartilage, or possibly by fibrous tissue.

What is the explanation of this curious condition? How are we to explain the presence of the triangular piece of bone? It is on this point that the anatomists can, I think, help the surgeons. The factors, according to Elmslie, that have to be considered as possibly playing a part in the causation of the condition are trauma, either at birth or later, and rickets. The latter can be dismissed at once: this deformity has no connection whatsoever except by accident with rickets. The deformity can apparently arise as a result of injury, since Elmslie mentions a case of Joachimstal in which the history of trauma was very definite, but it is inconceivable that trauma could produce identical lesions in both femoral necks, either during the birth of a child or later. To my mind the close symmetry seen in the bilateral cases puts trauma entirely out of court. That a condition closely resembling this may be seen after injury only goes to prove that similar abnormal appearances may result from different causes. I venture to suggest that this condition is really a congenital developmental error, the coxa vara deformity being secondary to this. It amounts to this, that the diaphyseal spur, as Prof. Walmsley calls it, which plays such an important part in supporting the femoral head, is ossified from a separate centre and not by direct extension from the shaft. It is possible that more than one nucleus of ossification may contribute to the formation of this separate fragment in some cases, since some of the radiograms seem to suggest this. My reasons for suggesting developmental error to explain the deformity are these:

1. Some error in gait is often noticed when the child begins to walk. In 4 of my 18 cases there is a definite history of something being wrong about the end of the first year, the history in several others being very vague and indefinite, and certainly not against this theory.

2. The deformity is extraordinarily symmetrical in bilateral cases. The abnormal clear line running through the neck is seen in precisely the same situation in both femora.

3. It is sometimes met with in association with other developmental errors, e.g. it has been seen in that curious condition called cranio-cleido-dysostosis. In this condition the skull is ossified late or imperfectly, and the clavicles are each represented by one or two separate pieces, or these bones may be entirely absent.

This radiogram (fig. 5) is taken from a case of dysostosis aged 6 years, kindly transferred to me for treatment by my colleague Mr Barrington-Ward, and shows the condition discussed here. Besides the triangular fragment and

the coxa vara, it shows the femoral heads are lying low in the acetabula, and the ossific centres for the heads are encroaching on the necks above, while in addition the pubes show no sign of ossification whatsoever. On examination of the patient the symphysis pubis seemed to be well formed, so presumably the pubes are cartilaginous. This case shows other abnormalities of the skeleton, to which attention was directed by Mr Barrington-Ward when he showed another case before the British Orthopaedic Association in 1924. The errors in that case, aged 3½ years, were:

(*a*) No ossification of the parietal bones.
(*b*) Double centres for the epiphyses of metacarpals and phalanges.
(*c*) No ossification in pubic bones.
(*d*) Two small centres for the clavicles—ununited.
(*e*) Delayed fusion of the mandible and neural arches.

In that case there was no coxa vara.

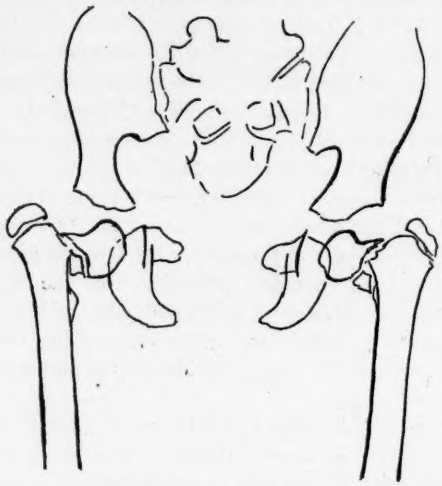


Fig. 5. Bilateral infantile coxa vara with absence of ossification in pubes.
(Case of cranio-cleido-dysostosis; girl aged 6 years.)

However, Mr Irwin of Belfast sent me radiograms of a third case of dysostosis which showed typical cervical coxa vara in addition to the other abnormalities, so that in two of the three cases coxa vara of the type under consideration was found.

Unfortunately there is no certain evidence, so far as I know, of cervical coxa vara being present at birth. When the condition of the upper end of the femur in the early months of life is remembered, it is not surprising that no radiographic evidence of this congenital abnormality in young infants is forthcoming. The youngest case I have met with was aged 2¼ years, while another

was 3 years old. So far as I know abnormal ossification of this type in the neck of the femur is not mentioned in the text books on Anatomy. The only condition I am familiar with which in the least resembles it occurs at the lower end of the femoral diaphysis where occasionally one sees a corner, adjacent to the lower epiphyseal line, separated from the rest of the metaphysis. If my suggestion is correct, and this is a developmental error, it seems to me possible, even probable, that the ossification of the diaphyseal spur by a separate centre is normal in one or more species of the lower animals. Supposing this buttress of bone were ossified separately but later fused with the rest of the neck and with the head of the femur, the unusual method of ossification might easily be overlooked even by those familiar with the skeleton of the particular species concerned.

The difficulty experienced in obtaining information on this point has induced me to follow the suggestion of one of your members and bring the subject before you to-day.

*Note.* The author would be very grateful to any anatomist who can throw light on the nature of this condition, if he would be kind enough to communicate with him.

# A NOTE ON THE SO-CALLED "DISUSE" ATROPHY OF MUSCLE

By N. ROSS SMITH, M.B., Ch.M. (Sydney), F.R.C.S. (Eng.),
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It is generally held that inactivity of a muscle leads to rapid wasting. The "disuse" theory of muscular atrophy has been widely accepted since it was first enunciated in relation to denervated muscle by Reid(1), supported by Brown-Séquard(2), in 1848. The common observation that a normal muscle increases in size with exercise has led to the assumption that the reverse is true, namely, that muscular wasting is due to inactivity. The term "disuse" has been applied indiscriminately to atrophy after denervation, atrophy associated with disease of bone or joint, and atrophy following upon immobilisation of a limb for fracture, the correction of a deformity, or to impose rest.

The experiments of Langley(3) and his collaborators, Kato and Hashimotu, appear to show that atrophy after denervation, so far from being due to inactivity, is the result of excessive activity in the form of fibrillation; and that daily exercise of the muscle by electrically stimulated contraction cannot prevent the atrophy. Clinicians have noted that muscular wasting with bone or joint disease is more rapid and extreme than that which occurs with simple disuse of the limb. It is observable also that wasting is greater in a limb immobilised for a traumatic or inflammatory lesion than in one rendered inactive during treatment of a congenital deformity; and that wasting arising in these several ways is more extensive and permanent in adults than in children. These observations require further study; their bearing on the cause of muscular atrophy is doubtless important.

The condition of a muscle which is present in three specimens of congenital absence of the tibia in the Royal College of Surgeons museum, appears to throw some light on the subject. This muscle was noted by Sir Arthur Keith in a specimen he examined for Mr R. Ollerenshaw(4). I observed it subsequently in dissecting two other specimens during an investigation (in collaboration with Mr E. Laming Evans) into congenital defects of the tibia(5). In all three specimens, this muscle is attached solely to the shaft of the fibula, and was therefore presumably unable to shorten and functionless. In the description of the specimen (Teratological Series, No. 439.41) examined by Sir Arthur Keith, the muscle is stated to be as thick as an adult finger and healthy in appearance. In one of the specimens I examined (Teratological Series, No. 439.5), the muscle is a large fleshy-tendinous mass attached in its whole length to the front of the proximal two-thirds of the fibula. In the other specimen

Fig. 1. Specimen No. 439.5 (R.C.S. Museum, Teratological Series). The muscle described in the text is designated "peroneus."

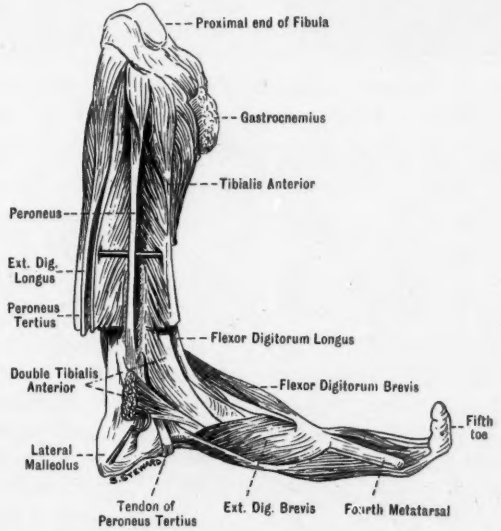


Fig. 2. Specimen No. 439.6 (R.C.S. Museum, Teratological Series).

(Teratological Series, No. 439.6) the muscle has a short fleshy belly arising from the front of the proximal end of the fibula, and a relatively long tendon running distally, in contact with, but unattached to the fibula until it reaches the distal end of the bone. Fleshy fibres are abundant in the muscle of both specimens, and there is no evidence, macroscopically or microscopically, of atrophy or degeneration. The accompanying drawings show the position and size, and the microphotographs the healthy state of the muscle. The muscle is designated "peroneus" in these specimens, but is more properly called "tibio-fibularis," as, according to Keith, it is a representative of that muscle.

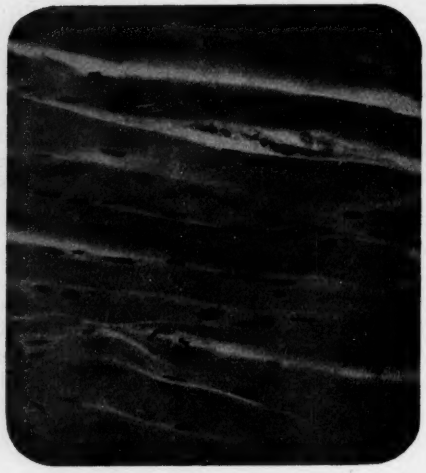

Fig. 3. Microphotograph of longitudinal section of muscle of specimen No. 439.5.

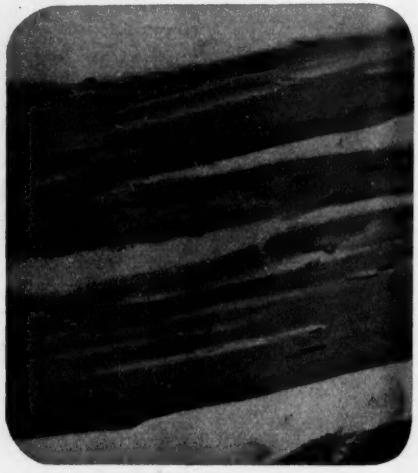

Fig. 4. Microphotograph of longitudinal section of muscle of specimen No. 439.6.

It appears that this muscle during life was unable to shorten, and subserved no function. Nevertheless it persisted without atrophy or degeneration. The ages of the patients at the time when the specimens were obtained by amputation, were two and thirteen years, respectively. The age of Ollerenshaw's patient is not given in his description, but the photograph is of a child of about ten years. There was therefore in all three cases abundant time for the occurrence of atrophy from disuse: that atrophy did not occur seems to throw some doubt on the disuse theory.

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(3) Langley, J. N. *Journ. of Physiol.* vol. xlix (1915), p. 432; vol. l (1916), p. 335; vol. lii (1918), p. 15; *Lancet*, ii (1916), p. 6; *Brit. Med. Journ.* ii (1920), p. 239.
(4) Ollerenshaw, R. *Journ. of Bone and Joint Surg.* vol. xxiii (1925), p. 528.
(5) Evans, E. Laming and Smith, N. Ross. *Archives of Disease in Childhood*, i, (1926) iv, p. 194.

# THE PROGRESS OF ANATOMY

By SIR ARTHUR KEITH

It is so uncommon in these days to come across a work in Anatomy which is at once new, stimulating and refreshing that the appearance of such a book deserves more than a passing notice. *Recent Advances in Anatomy*[1] by Dr H. Woollard, who has been appointed Elder Prof. of Anatomy, in the University of Adelaide, in succession to Prof. F. Wood Jones, is such a book; it takes us right off the beaten track and is particularly worthy of attention because it seems to the writer to point the way which British Anatomy is likely to take in the immediate future.

One cannot survey the course taken by British Anatomy during the past forty years without being struck with resemblances to that which holds for "gold-rushes." No sooner is some new and promising field announced than there is a desertion of the old field for the new—even if the old field be far from exhausted. Forty years ago British anatomists were employed on three fields: there was that of naked-eye anatomy of the human body—filling in the minutiae of descriptive details and studying variations and vestigial structures under the stimulus given by Darwin; there was the old field of comparative anatomy, and there was the newer field of microscopic structure. And now all these fields are forsaken—not because they are worked out, but because others for the time being have become more attractive. The old-fashioned British Anatomist is dead and has been replaced by men with other ideals, but there is one part of our ancient tradition which I hope is still alive—the determination to lay before the students of medicine a solid and systematic understanding of the structure of the entire human body. If we British Anatomists fail in this we shall have parted with the best part of our inheritance.

Late in the "eighties" of last century Wilhelm His of Leipzig opened up a new gold field and the younger anatomists of the time rushed to it. The exact methods introduced by Prof. His, particularly his art of reconstruction, opened up a new and most profitable field of knowledge; one cannot exaggerate the permanent gain we owe to him. Franklin Mall introduced the Leipzig method to Johns Hopkins Medical School and from there it passed into the medical colleges of the Unites States, replacing the old-fashioned methods to a much greater extent than was the case in Britain. In these earlier days we all rushed to Leipzig to see what Wilhelm His was doing; none of us stopped at Halle to learn what Wilhelm Roux was accomplishing. In the light of later events this is a strange fact.

[1] *Recent Advances in Anatomy*, (London: Churchill, 1927), pp. 302, figs. 77. Price 12*s*. 6*d*. net.

The field opened up by Wilhelm His is not exhausted; it is little more than roughly surveyed and yet already it is being deserted. The exodus was led by Franklin Mall's pupil, Ross Harrison, and I know of no more interesting movement in modern anatomy than that of which Ross Harrison was the central figure. In 1902 he was investigating the origin of nerve fibres and of their sheaths by the methods of Wilhelm His, but to obtain a more definite answer to his questions, adopted the experimental methods of Wilhelm Roux, and ultimately finding that they too failed him, introduced later in 1906 a new method—the method of the drop culture—unconsciously imitating the technique of the Bacteriologist. In twenty years the "drop-culture" has caused microtome and wax plates to retire from the central bench of anatomical laboratories and left "tissue-culture" in all its modern modes in chief possession. We have but to turn to Dr Woollard's book to see how this fresh field is being exploited and the new and profitable knowledge which is being gathered.

From Dr Woollard's book it will be seen also that most of the "advances" which he has chronicled have been obtained not by the opening up of a new field of enquiry—but by the return to an old field which anatomists should never have consented to leave—that of experimental enquiry. Looking back to the "seventies," "eighties" and "nineties" of last century, in the light of accumulated wisdom, one sees that the best anatomical results in England were being obtained by anatomists who looked upon themselves as physiologists. By the experimental method Ferrier was then revealing the anatomy of the brain; by the same or allied means, Gaskell, Langley, Sharpey-Schafer, Horsley, Mott, Sherrington and Head were "dissecting" the nervous system. Most of the advances which Woollard has to describe have been obtained by the application of the experimental method.

What really has happened recently, and is happening now, is the desertion of the fields of "dead" anatomy for those of "living" anatomy by our younger men; they have resolved, or are resolving, to apply themselves to the study of structures in a living state, and beyond a doubt if the new knowledge is happily combined with the old Anatomy, medical students will gain immeasurably by this departure. The methods of enquiry which are finding favour with younger men are those which bring them into touch with living process. It is thirty years since Röntgen placed a new method in our hands of investigating the structure of the living body, but anatomists generally were slow to understand the power of even the earlier imperfect appliances; with improved technique Röntgen rays became one of the most potent means of anatomical advance. The method of vital staining goes back to the earlier part of the eighteenth century when Belchier, a surgeon of Guy's Hospital, studied the action of Madder—but the development of this method is altogether modern. It seems only yesterday when Goldmann, the Heidelberg surgeon—a native of South Africa—came round the laboratories of England and enthusiastically demonstrated his "Pyrrhol" cells—although it must be

in reality about seventeen years ago, and later came Prof. H. M. Evans who has done so much to extend the method of vital staining and to place it on a scientific basis. And last of all, but not least, comes the new field opened up by Dr R. Chambers of Cornell University, making it possible for the anatomist to dissect a living cell of microscopic dimensions, and thus bringing within reach of British anatomists the privilege of turning to vivisection without being obliged to obtain a licence from the Home Office.

Dr Woollard has done a service to Anatomy, particularly to British Anatomy, by bringing together the "advances" which have been made by anatomists using all of these newer methods. It is but natural he should confine the scope of his survey to schools and to men with whom he himself has been in contact, but it would be an injustice to British, French, German and many American Anatomists were readers to believe that the narrative written by Dr Woollard includes the whole harvest of advance made in recent years.

# REVIEWS

*Cunningham's Manual of Practical Anatomy.* Revised and edited by Arthur Robinson. Eighth edition. In three volumes. Volume I, pp. xxx + 451, 210 figures. Volume II, pp. xxx + 524, 233 figures. Volume III, pp. xxx + 568, 237 figures. (London: Humphrey Milford, Oxford University Press, 1927.) Price 12*s.* 6*d.* net, per volume.

The editor, the artist and the publishers are all to be congratulated on the appearance of the eighth edition of this deservedly popular dissecting manual.

The book is again issued in three volumes, but it is good to see that the size of each volume remains unchanged, and one hopes that stability in this respect has again been attained. The B.N.A. terminology is retained, as one had expected, and the editor gives four very cogent reasons for its retention. But, if the book remains unchanged so far as size and terminology are concerned, it has been enriched by a number of new coloured plates, examples of the best work of Mr J. T. Murray, whose drawings of anatomical subjects are as truthful as they are artistic.

Relatively little change has been made in the letter-press, but, despite what has been said about the size of the book, one would welcome more frequent references to the functions of the various structures, whose topographical anatomy is described so admirably and so fully. No teacher of anatomy at the present time would commence a lecture or a demonstration on the Thalamus, for example, without first indicating the importance of its position on the sensory path from the periphery to the cortex. It is true that the book is, in name, a dissecting manual, but it has become, largely as a result of sheer merit, the main standby of the medical student so far as Human Anatomy is concerned, and it is a pity that the opportunity of associating function with structure should be left almost entirely to the teacher.

*Die Entwicklung des Menschen vor der Geburt.* By Prof. med. Ivar Broman, Direktor des Anatomischen Instituts der Universität Lund. (Munich: Bergmann), 1927, pp. 351, figs. 259. Price 26·40 Marks.

We consider this to be one of the best, if not the best, of the elementary treatises on human embryology. It is written by one who is better qualified for the task than any other anatomist in Europe. The illustrations, about 400 in number, are accurate and well executed and the text is based on a first-hand knowledge. It is clearly written. The present work is supplementary to the *Grundriss der Entwicklungsgeschichte des Menschen* which Prof. Broman published in 1921, but we regard the present book as the more suitable for students of Medicine.

# ON THE BRAIN OF THE MACROSCELIDIDAE
## (*MACROSCELIDES* AND *ELEPHANTULUS*)

By Professor W. E. LE GROS CLARK, F.R.C.S.
*Medical College, St Bartholomew's Hospital*

The elephant shrews are of particular interest to morphologists, partly because they form a family usually grouped with the Tupaiidae in the sub-order Menotyphla which is believed by many authorities to bear an important relation to the forerunners of the primate phylum, and partly because these Insectivores display in their anatomical structure a number of remarkably primitive and metatheroid features which have from time to time been noted by zoologists. Of all these features, the brain of *Macroscelides* appears to be unique amongst Mammals. In 1902, Elliot Smith (13) drew attention to this interesting point. He described the astonishing development of the hippocampal formation and the curiously metatheroid psalterium and noted the association of these primitive features with a small ventral commissure and an elongated and Primate-like corpus callosum. The unusual conformation of these parts of the brain, together with the uncertainty regarding the systematic position of the Macroscelididae which still exists, has prompted me to carry out in as complete a manner as possible a detailed study of the brain.

The original genus of *Macroscelides* was divided by Oldfield Thomas (15) in 1906 into three separate genera, mainly on the basis of the characters of the molar teeth and the tympanic bulla, *Macroscelides*, *Elephantulus* and *Nasilio*. This communication deals with the brain of the first two genera.

### MATERIAL

I have to express my great indebtedness to the Director of the Transvaal Museum, South Africa, for having sent me three specimens of *Elephantulus myurus jamesoni*, in two of which the brains were excellently preserved. These brains have been studied macroscopically, and from them the text-figs. 1 to 4 have been prepared. To Prof. Elliot Smith I owe gratitude for a complete series of transverse sections through the brain of *Macroscelides* (species unknown) which had been sent to him by Dr Broom. These sections had been stained with a combination of Weigert-Pal and neutral red, with very good results. The fine medullated fibres are sharply delineated and the cyto-architecture can also be readily studied in the same sections as a result of the neutral red staining. I wish to thank Prof. Elliot Smith, also, for reading through this paper before publication. Owing to the kindness of Sir Arthur

Keith, I have also been able to study the brain of a specimen labelled *Macroscelides* which had been preserved for many years in the museum of the Royal College of Surgeons. From this specimen the outlines of text-figs. 5 (*a*) and 9 were drawn. This specimen and the specimen from which the sections were prepared correspond accurately with the figures of the brain of *Macroscelides proboscideus* in Elliot Smith's original paper. It will be seen that there are notable differences in brain structure between *Macroscelides* and *Elephantulus*, the characteristic features of the brain of the Macroscelididae being more emphasised in the former than in the latter genus.

## GROSS ANATOMY

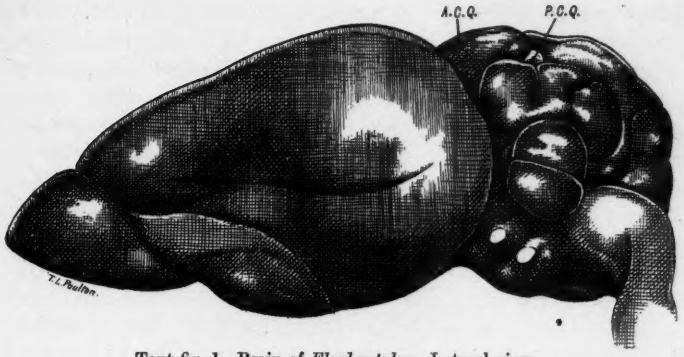
In general form, the encephalon of the Macroscelididae is relatively short and broad. The divergence of the cerebral hemispheres caudally with the exposure of the enormous anterior colliculi on the dorsal aspect of the brain is one of the most striking features of the undissected brain.

The following detailed account refers to the brain of *Elephantulus myurus jamesoni*.

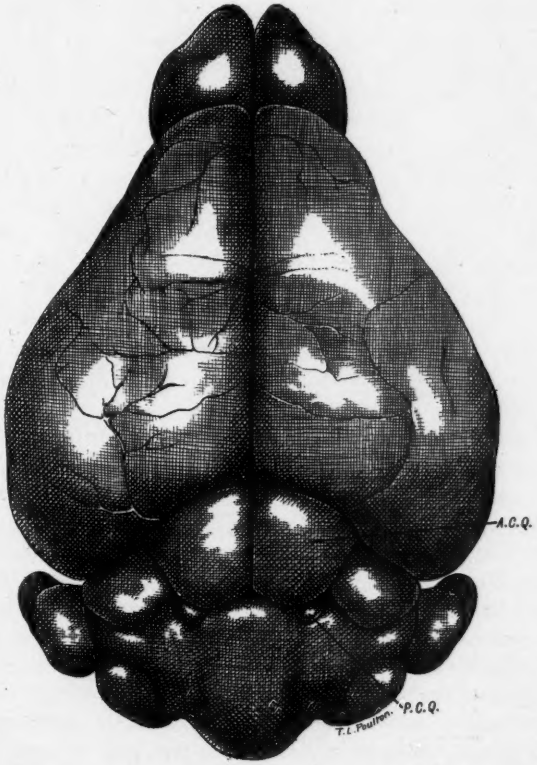
The weight of the brain as a whole amounted to 1·14 gm. The ratio of the brain weight to the body weight (35·8 gm.) works out at 1 to 31·4.

The *olfactory bulbs* measure 5·5 mm. in length (on their ventral aspect), and 3 mm. in breadth. They project beyond the extremity of the frontal poles for a distance of 2 mm. The bulbs, which are sessile, terminate in blunt points anteriorly and are closely pressed against each other. The ventral surface is only slightly inclined to the horizontal plane. The *fissura circularis* is shallow on the ventral surface where it separates the bulb from the tuberculum olfactorium, and on the dorsal part of its extent, it is joined by the rostral end of the endorhinal sulcus. If, however, the olfactory bulb is here drawn away from the frontal pole of the hemisphere, it may be seen that in the depths of the interval between them, the fissura circularis and the endorhinal sulcus remain distinct for a short distance to leave a small space for the dorsal olfactory tract. The fissura circularis shows a slight posterior concavity where it crosses the lateral olfactory tract.

The *tuberculum olfactorium*, viewed from the ventral aspect, forms an oblique oval with the long axis extending postero-laterally. It measures 4·5 mm. in length by 4 mm. in breadth. Its surface is not markedly convex and slopes laterally in conformity with the general contour of the piriform region. A broad shallow groove crosses the surface antero-laterally and serves to accommodate the optic nerve. The tubercle is limited laterally by the olfactory tract, while postero-laterally and posteriorly it is separated from this and from the locus perforatus anticus by an evident *fissura rhinalis arcuata*, in which a small blood vessel runs. The part corresponding to the *fissura diagonalis* of Beccari can be seen running antero-medially into the septal region.




Text-fig. 1. Brain of *Elephantulus*. Lateral view.
*A.C.Q.* Anterior corpus quadrigeminum. *P.C.Q.* Posterior corpus quadrigeminum.




Text-fig. 2. Brain of *Elephantulus*. Dorsal view. Lettering as in previous figure.

The *lateral olfactory tract* narrows gradually as it is traced caudally. From the olfactory bulb it extends backwards and a little outwards, and then, at the point where it is crossed by a blood vessel, and where the arcuate fissure first becomes apparent, it turns rather abruptly medialwards, ventralwards and backwards, fading out on the surface of the piriform lobe at the posterior extremity of the olfactory tubercle. At its termination, the surface of the piriform lobe is raised into a small and indistinct eminence, the elevation marking the position of the nucleus of the lateral olfactory tract. The fissura endorhinalis is not evident on surface view as a real fissure, its position being merely marked out by the lateral margin of the white olfactory tract.

The *rhinal fissure* runs more or less horizontally backwards. It becomes smoothed out at the site of the orbital depression on the hemisphere, and is thus divided superficially into two parts, anterior and posterior. The anterior portion terminates rostrally by fading away on the lateral surface of the frontal pole. It does not join the fissura circularis. The posterior portion of the rhinal fissure runs caudally with a faint downward convexity. Posteriorly it curves upwards and gradually disappears before it reaches the caudal margin of the cerebrum. It is continued on as a small vascular groove only. No clear indication of a *fissura rhinalis medialis* can be detected on the medial surface of the hemisphere.

The *piriform lobe*, traced from its anterior extremity, broadens out at first gradually, and then with some abruptness where the lateral olfactory tract turns medially. The surface of the lobe is curved in harmony with the orbital excavation of the ventro-lateral surface of the hemisphere. The most medial portion (as seen from the ventral aspect) which abuts on the tuber cinereum is marked off from the rest of the lobe by a short antero-posterior groove, the *fissura amygdalae*.

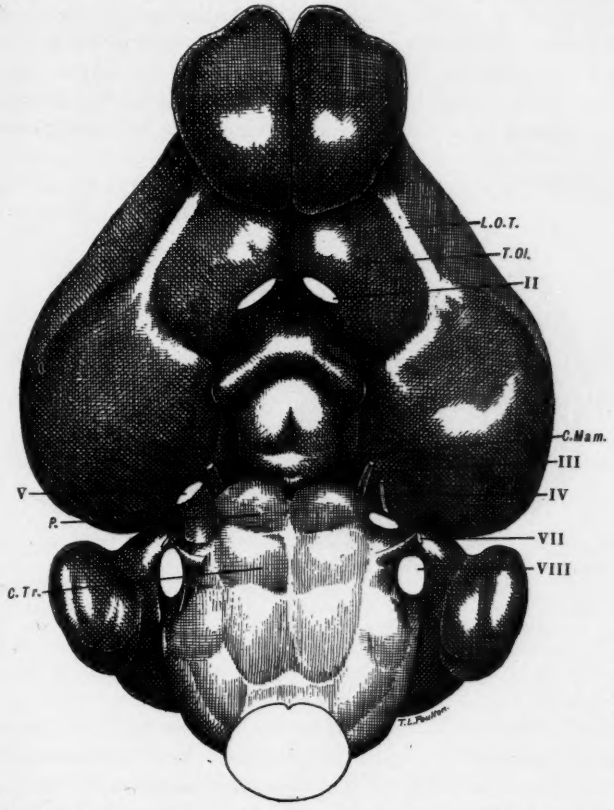
From the olfactory tubercle, the ventral surface of the piriform lobe slopes evenly upwards and backwards, and no definite natiform eminence is produced. The rounded surface lateral to the amygdaloid fissure corresponds to the position of this eminence.

The *neopallium* is smooth laterally and dorsally. The hemispheres rapidly narrow towards the frontal poles. The dorso-medial border measures about 10 mm. in length. The caudal margin of the hemisphere extends postero-laterally from the median line, with which it makes an angle of some 120°. Laterally the contour of the cerebrum is adapted to form a broad shallow orbital excavation.

The basal view (text-fig. 3) shows the *optic chiasma* to be of moderate size. Superficially no distinction can be made between the optic decussation proper and the commissure of Gudden as can be seen, for instance, in the brain of the mole (Ganser). The first millimetre or so of the optic tract can be seen before it dives under cover of the medial border of the piriform lobe, and it shows a faint groove where it comes into contact with the free border of the tentorium cerebelli.

A broad low convex *tuber cinereum* is seen behind the chiasma, and behind this, also visible in the undissected brain, a narrow pale band representing the mammillary region.

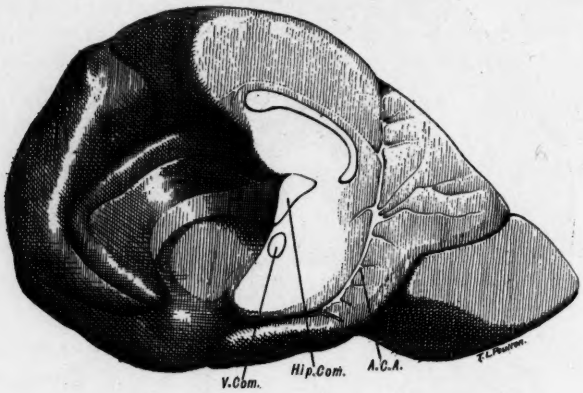
The *oculomotor nerve* is conspicuous as it emerges from under cover of the anterior border of the pontine region about 3 mm. distant from its fellow




Text-fig. 3. Brain of *Elephantulus*. Ventral view. *L.O.T.* Lateral olfactory tract. *T.Ol.* Tuberculum olfactorium. *C.Mam.* Corpus mammillare. *P.* Pons. *C.Tr.* Corpus trapezoideum. The cranial nerves are numbered.

and overhung by the medial border of the piriform lobe. Lateral to the commencement of this nerve the delicate trochlear nerve may be seen if the root of the large trigeminal nerve is carefully lifted. Immediately caudal to the tuber cinereum and the origin of the third nerves are two transversely oval elevations (text-fig. 3, *P*), one on either side of the mid-line, of a conspicuous reddish brown colour. These appear to bear a very close resemblance

to the ganglion infrapedunculare described by Ganser (5) in the brain of *Talpa*. A study of the transverse sections, however, indicates that this grey matter lies actually in the pons, the transverse fibres of which are spread out in a very thin layer over the surface of it. Behind the pons is the corpus trapezoideum, distinguished from the pons in front and the ventral surface of the medulla behind by its white colour. The pons and the trapezoid body are both deeply grooved in the mid-line by the basilar artery. Laterally, in the interval between the pons and the corpus trapezoideum issues the root of the trigeminal nerve, and postero-lateral to this the origin of the small seventh and the large eighth nerve. A glimpse of the tuberculum acousticum immediately lateral to the root of the acoustic nerve is also visible from this aspect.



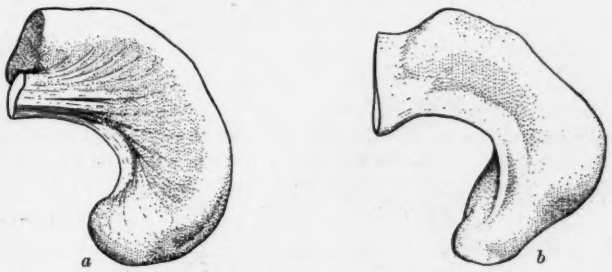

Text-fig. 4. Medial aspect of cerebral hemisphere of *Elephantulus* dissected to show the hippocampal formation. *Hip.Com.* Hippocampal commissure. *V.Com.* Ventral commissure. *A.C.A.* Anterior cerebral artery (groove).

On the dorsal aspect of the brain, the anterior colliculi (text-figs. 1, 2, *A.C.Q.*) are exposed to a considerable degree between the cerebrum and cerebellum. The exposed area of each colliculus measures 3 mm. anteroposteriorly and 3·5 mm. laterally. A small triangular portion of each posterior colliculus is also exposed to view in the undissected brain between the median and lateral cerebellar lobes.

*The medial surface of the cerebral hemisphere* (text-fig. 4). It is in the appearance of the medial surface of the brain that the main differences between the brains of *Macroscelides* and *Elephantulus* are to be seen. As before, this description applies mainly to the brain of *Elephantulus*.

The details of the commissures are perhaps one of the most interesting features of the brain of these animals, as Elliot Smith has already pointed out. The *corpus callosum* is elongated, slightly convex dorsally, and shows

a well-marked splenium with a splenial bend, a conspicuous genu, and a slightly bulbous rostrum. It measures about 4 mm. in length. Below it, but separated by a broad, flat, cut surface, is the fornix commissure which is of large size and approaches the crescentic shape so characteristic of Marsupials. The cut surface between these two commissures is formed (as can readily be seen by reference to the transverse sections (Plate I, figs. 16, 17)) by the relatively enormous dorsal extremity of the hippocampus, which here in an inverted form is closely pressed up against and actually fused with its fellow of the opposite side. In *Macroscelides* (text-fig. 9 *b*) this exaggeration of the subsplenial flexure is even more impressive, and the corpus callosum has been stretched out and thinned by the pressure of the hippocampus, so that in section it appears as an elongated strip approaching close to the dorso-medial border of the hemisphere. In this genus, also, the fornix commissure is more conspicuously metatheroid in shape.

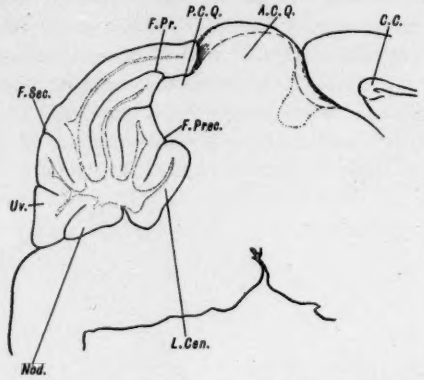



Text-fig. 5. The hippocampus and fornix of (*a*) *Macroscelides rozeti*, and (*b*) *Erinaceus*, dissected out and viewed from the antero-medial aspect to indicate the remarkable development of the subcallosal portion of the hippocampus in *Macroscelides*. (*a*) ×5. (*b*) ×4.

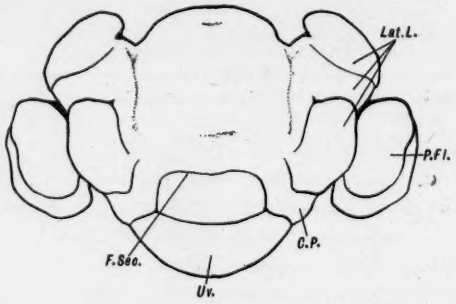
The ventral commissure lies immediately below the fornix commissure. Its small size is in marked contrast with the relatively large commissure found in the lipotyphlous insectivores. Below and in front of the anterior commissure is the paraterminal or septal region, fused across the mid-line as far forward as the level of the genu of the corpus callosum. Ventrally, this area is separated from the medial margin of the tuberculum olfactorium by the *fissura rhinalis arcuata*, from which emerges rostrally a large vascular groove which accommodates the anterior cerebral artery (text-fig. 4, *A.C.A.*). This groove ascends vertically, giving off branches, and just above the level of the corpus callosum divides into two main terminal branches, of which one courses dorsally to reach the dorsal aspect of the hemisphere, while the other runs back immediately above and parallel to the corpus callosum. On superficial inspection, this groove gives the corpus callosum the appearance of being much thicker than it really is.

With the removal by dissection of the mid-brain, the hippocampal formation is brought into view. The fimbria runs back from the hippocampal

commissure and terminates close to the ventral extremity of the extra-ventricular alveus. The latter forms a relatively broad band exposed on the medial aspect of the cerebrum. Below it expands somewhat to form a low flat hippocampal tubercle. Above it disappears immediately caudad of the hippocampal commissure by the fusion of the fimbrio-dentate with the




Text-fig. 6. Sagittal section through the mid- and hind-brain region of *Elephantulus*. ×5. *C.C.* Corpus callosum. *A.C.Q.* Anterior corpus quadrigeminum. *P.C.Q.* Posterior corpus quadrigeminum. *F.Pr.* Fissura prima. *F.Sec.* Fissura secunda. *F.Prec.* Fissura preculminis. *L.Cen.* Lobus centralis. *Uv.* Uvula. *Nod.* Nodule.




Text-fig. 7. Cerebellum of *Elephantulus*, viewed from the postero-superior aspect. ×5. *Lat.L.* Lateral lobe. *Pfl.* Paraflocculus. *C.P.* Copula pyramidis. *F.Sec.* Fissura secunda. *Uv.* Uvula.

fimbrio-alvear (of Obenchain) fissures. The dentate gyrus forms a simple uncrenated band of grey matter of fairly even width. It is sharply marked off from the neighbouring pallium by a continuous hippocampal fissure which at its ventral extremity turns forwards and ventralwards to limit ventrally the hippocampal tubercle. Immediately below the latter, a faint furrow runs horizontally backwards, the *fissura amygdaloidea medialis*.

The *cerebellum* (text-figs. 6, 7) is of a very simple type. In a sagittal

section, the main *fissura prima* and *fissura secunda* can readily be recognised. A very faint *fissura suprapyramidalis*, only evident superficially in the mid-line, separates the pyramid from the declive. The pars suprapyramidalis, which with the pyramid forms the lobus medialis of the cerebellum, is thus quite smooth. Faint antero-posterior depressions indicate the separation of the lobus medialis from the lateral lobes. The latter are each divided by well-marked but incomplete fissures into three folia of approximately equal size (superficially), of which the middle is in most direct superficial continuity with the middle lobe.

An inspection of the anterior surface of the cerebellum shows that the middle lobule is really the largest of the three. Its anterior surface, which is moulded round the lateral aspect of the posterior colliculus, is subdivided again into two folia by a vertical sulcus.

The pyramid is connected by a simple unfissured copula pyramidis with the paraflocculus. The latter is divided by a horizontal sulcus into two folia of which the upper is very slightly the larger. In front of and below the base of the paraflocculus is the simple unfissured flocculus, approximately equal in bulk to the upper folium of the paraflocculus.

Behind the fissura secunda is the *uvula*, divided superficially by a complete transverse sulcus reaching to the copulae pyramidis on either side. The *nodule* is not visible in the undissected brain but can be seen in sagittal section.

On the anterior surface of the cerebellum, a *U*-shaped *sulcus preculminis* separates the simple undivided *culmen* from the *lobus centralis*. The latter is again subdivided by a transverse sulcus. The *lingula*, seen in sagittal section, is hardly significant enough to be regarded as a separate lobe of the cerebellum.

## MICROSCOPICAL ANATOMY

The transverse sections of the brain of *Macroscelides*, on which the account in this section is based, were cut at a thickness of 15 $\mu$. The total length of the cerebral hemispheres occupied 967 sections.

### *Primary Olfactory Areas.*

A study of the sections indicates that the olfactory bulbs (Plate I, figs. 10, 11) in the brain from which they were prepared were complete. The bulbar formation can be traced back as far as Section 371, the frontal poles of the neopallium appearing at Section 162. Thus the bulb is about 5·5 mm. in antero-posterior extent and projects beyond the level of the frontal pole by 2·4 mm. There is no need to describe in detail the structure of the bulb, for it conforms in general respects to the structure of the bulb of other mammalian brains. In section, the bulb is a vertical oval, narrower ventrally. Anteriorly, it is surrounded on all sides by rootlets of the olfactory nerves which terminate in a conspicuous stratum glomerulosum. As the sections are traced back, the stratum glomerulosum disappears, first on the medial

half of the dorsal aspect of the bulb, the vomero-nasal nerve being left isolated in this position. At Section 145, the accessory bulb appears, that is, slightly rostrad of the frontal pole of the neopallium. The accessory bulb (Plate I, fig. 10, *Ac.B.*) shows the usual structure. It has a broad stratum moleculare filled with medium-sized pale staining cells, which are in continuity with the single layer of mitral cells of the bulb proper. Medullated fibres from the accessory bulb run laterally to contribute to the dorsal peduncle of the lateral olfactory tract. The stratum granulare of the accessory bulb lies deep (ventral) to these fibres, whereas in the rest of the bulb, this stratum is superficial to the fibres which collect to form the lateral olfactory tract. The position of the accessory bulb is marked on the dorsal surface by a very faint furrow.

*Secondary Olfactory Areas.*

In Section 156, a clump of medium-sized cells, pyramidal and angular in shape, appears dorsal to the central core of the bulb, ventral to the compact stratum granulare of the accessory bulb, and immediately in front of the anterior extremity of the ventricle of the bulb. This marks the commencement of the anterior olfactory nucleus of Herrick (Plate I, fig. 11, *N.O.A.*). Traced back, this mass of grey matter rapidly spreads down the lateral aspect of the olfactory ventricle and further posteriorly sends a medial limb down the medial aspect of the ventricle, forming an inverted *U* in the concavity of which lies the intermediate olfactory tract. The medial and lateral limbs eventually meet on the ventral aspect of the ventricle at Section 334 and thus complete the periventricular ring. From the inner aspect of this ring, fibres pour out into the intermediate olfactory tract. As described thus far, the anterior olfactory nucleus shows no differentiation. The only part of the anterior olfactory nucleus, using the term in Herrick's sense, that can be described as differentiated is the pars externus. This appears at Section 182. At this level, the lateral olfactory tract has the appearance of a query mark in transverse section, with the convexity laterally. Along the dorsal part of the inner concave margin of the tract a small compact group of cells, similar to those which form the main part of the anterior olfactory nucleus, makes an appearance. This is the pars externus (Plate I, figs. 11, 12, 13, *N.O.A.* (*p.e.*)). A few sections more caudally, where the lateral olfactory tract becomes exposed to the surface of the bulb on its dorsal aspect, this external nucleus slides down ventrally until it soon becomes a small localised clump of cells on the medial aspect of the ventral end of the lateral limb of the olfactory tract. Eventually it fades away close to the caudal limit of the bulbar formation. This well-defined cell group has been described in the opossum (Herrick)(7), rat and *Caenolestes* (Obenchain)(11). In the two former Mammals, the nucleus is described as being caudally swallow-tailed in shape. There is no trace of such a splitting of the nucleus in *Macroscelides*. Obenchain has discussed at some length the significance of this nucleus, and suggests

that it is some sort of reinforcing device, discharging its fibres into the subjacent lateral part of the anterior olfactory nucleus. Its diminutive size in relation to the massive lateral olfactory tract is hardly explicable on this hypothesis. In the sections here studied, the nucleus commences laterally in very close association with the accessory bulb, its cells actually intermingling with the cells of the stratum granulare of the accessory bulb. It is forcibly suggested to one that this external nucleus is related to the accessory bulbar formation in the same way that the main bulk of the anterior olfactory nucleus is related to the bulb proper, and that it slides down the lateral olfactory tract in association with the fibres contributed to this tract by the accessory bulb.

If the different parts of the anterior olfactory nucleus are traced caudally in the sections, they are found to behave as follows. The pars dorsalis becomes lodged in between the extreme rostral end of the anterior hippocampal formation and the anterior piriform cortex. Here it forms a conspicuous mass of cells lying ventral to the anterior extremity of the centrum ovale. This mass soon disappears, however, and gives way to a relatively cell-free zone which in turn is replaced by the anterior horn of the lateral ventricle. The pars dorsalis thus appears to maintain its individuality until it disappears altogether, and it would not be correct to say that it merges with the cell mass of the frontal pole of the neopallium. The pars lateralis becomes continuous with the anterior piriform cortex, but when these two formations first come into contact, they are separated by a dipping in of the lamina zonalis at a level which corresponds to the dorsal margin of the main mass of the lateral olfactory tract. In this region, the cortex of the piriform lobe is readily distinguishable from the pars lateralis of the anterior olfactory nucleus, for its cells are more compactly and regularly arranged in a narrow superficial band, they are more pyramidal and more darkly stained. Close to the posterior end of the bulbar formation, the distinction between piriform cortex and pars lateralis disappears. At Section 291, where the pars medialis abuts on the cortex of the medial surface of the frontal pole of the neopallium, a small condensation of moderately large pyramidal cells appears, the rostral extremity of the cortex hippocampi. With this anterior hippocampal formation and the undifferentiated "primordium hippocampi" of Johnston the pars medialis becomes continuous.

The ventral part of the anterior olfactory nucleus is prolonged back as the pars posterior between the tubercular cortex and the head of the caudate nucleus (Plate I, fig. 15, *N.O.A.* (*p.p.*)). When these latter structures first appear rostrally, the pars posterior expands somewhat to form a conspicuous mass of polygonal cells notably larger than the cells which form other parts of the anterior olfactory nucleus. Among these cells stream the medullated fibres of the olfacto-septal and olfacto-cortical tracts. More caudally, the pars posterior becomes flattened out as though by pressure of the superjacent head of the caudate and its cells become gradually replaced by the small

granules of the tuberculum olfactorium. It should be noted that there appears to be no continuity between the tubercular cortex and the anterior olfactory nucleus, the one becomes replaced by the other in a manner which is quite abrupt in spite of the fact that the cells of the two formations intermingle somewhat at their junction. In *Orycteropus*, Woollard (18) notes that the anterior olfactory nucleus forms a definite cortex with a wavy outline, and that this cortical layer appears to run directly into the tubercular cortex.

The olfactory tracts in these sections need not be described in any detail. In their origin, course, and destination they conform to the usual mammalian condition. The medial olfactory tract is small and ill-defined.

The *tuberculum olfactorium* (Plates I, II, figs. 15–19, *T.Ol.*) first shows itself at Section 379 and the last traces of it are seen posteriorly at Section 592. Anteriorly it commences on the ventral aspect of the pars posterior of the anterior olfactory nucleus, and as it is traced caudally, it extends evenly in a medial and lateral direction. The medial limb at first extends vertically upwards in the septum, close to the surface. This presumably corresponds to the nucleus of the medial olfactory tract of Livini. Further back, it sends up a prominent process which lies on a deeper plane, and, running between the nucleus accumbens and Johnston's medial parolfactory nucleus, expands into a club-shaped extremity which actually reaches the ependymal layer of the lateral ventricle at Section 450. The tubercular cortex shows the usual structure, being composed of small, round, darkly-staining cells which are arranged in a slightly wavy outline and here and there collected into clumps forming the characteristic islands of Calleja. A short distance behind its rostral margin, cells of a similar type appear, forming a narrow layer in close contact with the convex ventral margin of the head of the caudate nucleus, so that in this region the pars posterior of the anterior olfactory nucleus appears sandwiched between a dorsal and ventral lamina of cells characteristic of the tuberculum. A study of the sections suggests that this dorsal lamina represents a rostral extension of the small-celled element of the basal amygdaloid nucleus (*vide infra*). Further caudally, the dorsal lamina disappears and soon after this the last remaining portion of the anterior olfactory nucleus, so that the caudate nucleus becomes covered by the tubercular cortex, only separated by a fine felt-work of medullated fibres which appear partly to contribute to the formation of the medial fore-brain bundle. The latter formation is certainly not at all conspicuous in these sections. The organisation of the olfactory tubercle in *Macroscelides* is not so complex either in the irregularity of the tubercular cortex or in the degree of differentiation of its cellular elements as is indicated by Obenchain for *Caenolestes*, and it also appears simpler when compared with Johnston's figures of this region in the opossum (8).

These sections provide no certain evidence for the still-disputed question as to whether the olfactory tubercle receives secondary olfactory fibres.

*The septal region.* Immediately rostrad of the anterior extremity of the corpus callosum the anterior hippocampal formation appears. Below the genu of the corpus callosum (Plate I, fig. 14, *A.H.*) it becomes well differentiated, and a conspicuous cortex of ammon pyramids, four or five cells thick, appears. Further back, this becomes replaced by a relatively thick undifferentiated mass, the lateral parolfactory nucleus of Herrick, or Johnston's primordium hippocampi (Plate I, figs. 15–17, *N.P.L.*). In so far as this mass represents the residue of undifferentiated tissue, out of which the anterior hippocampal formation appears to be differentiated dorso-medially, Johnston's term may have some basis of justification. Dart's criticism of the term, however, seems a very pertinent one, and for this reason, Herrick's nomenclature is undoubtedly preferable. Lower down, in the pars inferior of the paraterminal body, is the medial parolfactory nucleus, consisting of scattered medium-sized, pale-staining cells in among which numerous septal fibres run (Plate I, figs. 15, 16, *N.P.M.*). Posteriorly, at Section 502, the cells at the ventral extremity of this ill-defined nucleus congregate at the medial aspect of the olfactory tubercle to form a conspicuous *nucleus of the diagonal band* (Plate I, fig. 17, *N.D.B.*). There is thus no line of demarcation between the latter nucleus and the medial parolfactory nucleus. The pars superior of the paraterminal body fuses with that of the other side at Section 442, relatively far forward, and this fusion proceeds ventrally as the tubercular cortex shrinks down from the medial surface. Thus the nucleus of the diagonal band never lies under the free medial surface of the cerebral hemisphere. Ventro-laterally, the nucleus is demarcated off superficially from the olfactory tubercle by a distinct fissura rhinalis arcuata. The *nucleus accumbens* is prominent as a portion of the caudate nucleus lying medio-ventral to the lateral ventricle (Plate I, figs. 15, 16, *N.A.*). It may be noted that in these sections it shows no characteristics beyond its relative position by which it can be distinguished from the main mass of the caudate nucleus, and there appears here to be no justification for dignifying it with a special name. There is no evidence in these sections of the presence of the olfacto-frontal bundle described in *Caenolestes* by Obenchain (11), and which is believed in that animal to represent Edinger's septo-mesencephalic tract of lower vertebrates.

*The amygdaloid complex.* Like other workers in this field, I have relied very largely on Johnston's detailed account for an analysis of the amygdaloid complex in my sections of the brain of *Macroscelides*. It will probably be most convenient to study the constitution of this complex from behind forwards. The amygdaloid complex commences at Section 825. Here, at the most dependent part of the temporal horn of the lateral ventricle, the cortex ammonis is to be found turning sharply lateralwards on to the ventral aspect of the cerebrum to become continuous with a somewhat diffuse layer of medium cells resembling in formation the zona presubicularis. This irregular cortical layer becomes slightly infolded towards the ventricle floor, and the site of this infolding is marked a little further forward by a faint surface furrow

(*fissura amygdaloidea medialis*) which serves superficially to separate the cortical amygdaloid nucleus from the lower margin of the hippocampal formation. The cells which appear to have migrated inwards from the surface at the site of this furrow form the medial amygdaloid nucleus which Johnston (8) has described in mammalian brains (Plate II, figs. 21–24, *N.A.M.*). This nucleus is continued laterally into the cortical amygdaloid nucleus whose cells are rather larger, and, caudally, are arranged fairly regularly in a cortical layer. More anteriorly, the cells of the cortical nucleus lie in a more diffuse layer. At the junction of the cortical nucleus and the piriform cortex, there is only the faintest suggestion of an amygdaloid fissure (the caudal prolongation of the fissura endorhinalis), but the turning inwards of the superficial cells at the junction of these two areas to connect up with the large basal nucleus is quite evident. This is in support of Johnston's view that the basal nucleus has been derived from an infolding of the medial margin of the piriform cortex.

The lateral amygdaloid nucleus (Plate II, figs. 19–23, *N.A.L.*) appears at the very caudal extremity of the amygdaloid complex as a well-defined oval group of medium pyramidal and polygonal cells which stain fairly deeply, lying up against the ventro-lateral wall of the ventricular cavity. Traced forwards, the lateral nucleus increases rapidly in size and soon forms a prominent elevation in the floor of the lateral ventricle. It is bounded laterally by the external capsule and in its posterior part by an extension downward of the cavity of the lateral ventricle which here separates it from the piriform cortex. In this region, therefore, the lateral nucleus projects relatively freely in the cavity of the ventricle, covered on its medial and lateral aspects by the ependymal lining of the ventricle. Ventrally, it is separated from the medial and cortical nuclei (at its caudal extremity) by prolongations of the external capsule. Rostrally, the lateral nucleus is continued as a darkly staining band of cells pressed up against the lateral surface of the putamen, and can be traced forwards as far as Section 568, at the level of the anterior commissure and well in front of the level of the posterior margin of the olfactory tubercle. In the anterior half of its extent, the lateral nucleus is traversed dorsally by fibres from the internal capsule. The large bulk of the lateral nucleus in *Macroscelides* is very impressive. Johnston notes that this nucleus is massive at its anterior end in the bat (*Myotis*) and that in the monkey (*Macacus*) it projects forward to an unusual extent.

The large-celled basal nucleus (Plate II, figs. 20–22, *N.A.B.* (*m.*)) appears first at Section 724, lying ventral to the medial extremity of the transversely oval lateral nucleus. Traced forwards, the basal nucleus is found to extend ventrally to the junction of the piriform cortex and the cortical amygdaloid nucleus as already mentioned, and here it appears to come into structural continuity especially with the piriform cortex. Medially to the basal nucleus lie scattered medium and small cells, forming the central nucleus through which run the caudally directed fibres of the stria terminalis.

Ventrally, the central nucleus is continuous with the medial amygdaloid nucleus. Ventro-medial to the anterior part of the basal nucleus is found a clump of small darkly-staining granule cells, and separated from the large-celled basal nucleus by a fibre layer. This would appear to represent the small-celled element of the basal nucleus in the rabbit's brain, described by Johnston (Plate II, fig. 20, *N.A.B.* (*p.*)). Traced caudally, these small cells wander medially to take up a position ventral to the central nucleus, still separated from the large-celled basal nucleus by a fibre layer. Eventually, further back, they come to lie up against the ventro-lateral wall of the ventricular cavity, dorsal to the medial nucleus and medial to the large-celled basal nucleus. Here, its cells tend to group themselves into clumps, and, as Johnston notes for the accessory basal nucleus which he describes in the brain of the opossum, bear some resemblance to the formation of the islands of Calleja. I am in some doubt, however, as to the identity of this small-celled group in the caudal region of the amygdaloid complex of *Macroscelides* with Johnston's accessory basal nucleus. It would be a matter of some interest to arrive at a definite conclusion, for Johnston states that this accessory nucleus is found in Marsupials and not in eutherian mammals, and although not a Marsupial, *Macroscelides* presents a number of curiously metatheroid features in its anatomical structure.

Rostrally, the small-celled basal element extends further than the large-celled element, and comes to lie immediately ventral to the lateral nucleus. It appears to be continued forward as small detached clumps of cells to the region of the olfactory tubercle where similar cells are found lying ventral to the head of the caudate nucleus and dorsal to the pars posterior of the anterior olfactory nucleus.

At Section 648, the well-defined nucleus of the lateral olfactory tract appears (Plate II, fig. 20, *N.L.O.T.*) to fade away again anteriorly at Section 609. It replaces the medial nucleus in position. There is no small-celled element of this nucleus as described by Obenchain for *Caenolestes*, but the middle of the nucleus is divided into two large-celled parts as described by Woollard (18) for *Orycteropus*, the main ventral element, and a small less circumscribed element consisting of cells of the same type as the main portion, intermingling with the caudal ramifications of the commissural bundle of the stria terminalis. The nucleus, though very clearly circumscribed, is not conspicuously large. It is certainly relatively smaller than the lateral olfactory nucleus of the opossum. The basal and central nuclei become indistinct at about Section 635, and fade away into the structure of the globus pallidus and diagonal band nucleus.

*Fibre connections of the amygdaloid nucleus.* The stria terminalis can be followed throughout its course, but an analysis of its constituent bundles cannot be made from these sections. The most conspicuous and well-defined element to be seen is the fasciculus which runs caudally to the lateral olfactory nucleus, Johnston's commissural bundle. It was not found possible to trace

the bed of the stria in an uninterrupted course from the bed of the anterior commissure back to the amygdaloid nuclei.

*The piriform lobe.* Rostrally the pars lateralis of the anterior olfactory nucleus is directly continuous with the piriform cortex. The latter, when it first appears anteriorly, is composed of small subpyramidal cells which are somewhat diffusely arranged to form a broad band comprising the second and third layers of the cortex. Traced caudally, the more superficial cells, forming the second layer, become smaller, more darkly stained, and more compactly arranged, while the larger pyramidal cells of the third layer become scattered over a broader zone. Thus the area piriformis anterior of Gray passes quite indefinitely into his area medialis. This latter area is essentially similar to the corresponding area which Gray has described in *Didelphys* (6). Lying above the caudal extremity of the area medialis is a small patch which corresponds in structure with Gray's area posterior (text-fig. 9 (*b*), *J*). It shows a looser arrangement of the cells forming the second layer and the addition of a fourth layer. The latter extends also for a short distance into the dorsal margin of the area medialis. The superficial cells of the area posterior are more darkly stained than those of the area medialis. No pale giant cells were observed in the area posterior, such as have been recorded by Obenchain (11) in the brain of *Caenolestes*. The area posterior first appears anteriorly at about Section 680 (Plate II, fig. 21, *A.P.P.*) and in the region of Section 750 the rhinal fissure disappears. At this level, also, and no doubt resulting in the disappearance at this point of the rhinal fissure, the lateral cortex appears much compressed and thinned out by the huge subjacent hippocampus, so that the dorsal limit of the area posterior is not easy to demarcate. This difficulty is enhanced by the fact that the structure of the area posterior closely approximates to that of the neighbouring neopallial cortex. The area extends over on to the medial surface of the cerebrum to a very small extent where it abuts on the area presubicularis and the hippocampal-amygdaloid junction. This specialised area posterior, according to Cajal, does not receive fibres directly from the lateral olfactory tract and may be regarded as subserving entirely associational functions. In *Macroscelides* it is of very small extent compared with *Didelphys*, but it is developed to relatively the same extent as it is in *Caenolestes*. The other divisions of the piriform area described by Gray can also be observed in this brain, but except for the area subpiriformis, they are hardly definite enough here to deserve separate names.

*The hippocampal formation.* Rostrally, the anterior hippocampus begins at Section 280 as a short band of small pyramidal cells continuous with layer 2 of the frontal neopallial cortex but more lightly stained than the neopallial cells (Plate I, figs, 13, 14, *A.H.*). This band extends ventrally to meet the anterior olfactory nucleus at the junction of the pars medialis and pars dorsalis. The cortex hippocampi anterior bends round ventral to the genu of the corpus callosum for a short distance. Here it forms a conspicuous band stretching in a vertical direction from the corpus callosum down on to the

surface of the medial parolfactory nucleus. At its dorsal extremity, close to the callosal fibres, is differentiated a clump of closely-packed small cells representing the gyrus dentatus formation in this region. These cells are slightly dislocated from the line of hippocampal cells ventrally by a suggestion of the interpositio medialis. Above the corpus callosum, the hippocampal formation disappears entirely except for a few pale-staining pyramidal cells pressed against the mid-dorsal line of the corpus callosum. These cells, which never amount to more than ten or so in each section, are not always visible, and indeed disappear altogether over the caudal part of the corpus callosum. There is thus no well-defined indusium and the striae longitudinales are not visible. The atrophy of the supracallosal hippocampus has been carried to an extreme. The hippocampal commissure is relatively large. These sections show no sharp distinction between the psalterium dorsale and ventrale, though the ventral fibres are less dense than the dorsal fibres of the commissure. Among the fibres, especially those of the ventral part, are numerous small cells forming the nucleus proprius fornicis (Plate I, fig. 17, *N.P.F.*). Precommissural fibres are evident, passing down in front of the ventral commissure into the septal region (Plate I, fig. 16, *F.Pr.*). Immediately ventral to the fornix commissure are the descending columns of the fornix (Plates I, II, figs. 17–23, *D.C.F.*). Traced posteriorly, these are found to run directly backwards until they lie under the ependymal lining of the third ventricle. Just behind the level of the ventral commissure many of their fibres pass into the habenular region, forming the fasciculus rhinencephalo-habenularis, and the descending columns then pass down through the substantia grisea centralis of the third ventricle towards the corpora mammillaria. Projecting for a short distance between the descending columns of the fornix above the ventral commissure and ventral to the fornix commissure is the recessus inferior.

The outstanding feature of the hippocampus of *Macroscelides* is the inordinate development of its subcallosal portion, and especially the intraventricular alveus. The extent of this development is illustrated by the sections and the illustration of the hippocampus which has been dissected from the lateral ventricle (text-fig. 5). The lateral ventricle is distended by the ammon's horn to an astonishing degree, and this has led to a stretching and thinning out of the overlying neopallial cortex, so that the latter in parts appears atrophic. The intraventricular part of the hippocampus reaches rostrally as far as the anterior end of the corpus callosum, fitting closely into the concavity of the genu. This huge subspenial flexure has led to a complete separation of the corpus callosum from the fornix commissure. Elliot Smith (13), owing to the condition of the brain on which he based his account, was unable to state what connection really exists between the two commissures, but he surmised the possibility that the bridge might not contain any nerve fibres, thus realising the condition found in the *Hapalidae*. These sections indicate, indeed, that no transverse fibres run through this bridge. Dorsal to the

massive hippocampus in the mid-line and ventral to the corpus callosum, is a band of well-medullated fibres running antero-posteriorly and forming the *fornix longus* (Plates I, II, figs. 17–19, *F.L.*). Anteriorly, just caudal to the genu of the corpus callosum, these fibres pass ventrally between the two hippocampal formations to join the other fornix fibres in the region of the psalterium. Caudally, the fibres of the fornix longus become sandwiched in between the two layers forming the splenium of the corpus callosum, and eventually they disappear at about Section 640. The corpus callosum has been stretched out into an attenuated lamina by the pressure of the large hippocampus to a degree which is much more marked in *Macroscelides* than in *Elephantulus*, and this displacement dorsally of the callosal fibres has led to further displacements in the neopallial cortex as will be seen later. The hippocampal formations of either side, between the corpus callosum and the fimbria, are closely pressed together and fused in the mid-line. Such a fusion is to be seen in the subsplenial flexure in other mammals, e.g. the rabbit, but in no mammal has this condition reached the development seen in *Macroscelides*. The extraventricular alveus forms a relatively broad band which runs down within the concavity of the gyrus dentatus on the medial surface of the hemisphere, and terminates below in a low rounded hippocampal tubercle (text-fig. 4). Here the hippocampus becomes exposed on the surface and runs into the cortical amygdaloid nucleus but separated superficially by a very shallow furrow, representing the *fissura amygdaloidea medialis*. Posteriorly there is a slight recurving of the hippocampal formation to form a temporal pole, so that in a few sections the hippocampal figure is shown twice in the same section. The dentate gyrus is thus duplicated for 68 sections (815 to 748), and the hippocampus for 24 sections only (760 to 737). This slight degree of curvature is a little more pronounced than in *Caenolestes*, in which the gyrus dentatus is alone involved in this hippocampal reversal.

The almost complete disappearance of the supracallosal hippocampus and atrophy of the indusium must be attributed to the pressure exerted by the phenomenal development of the subcallosal portion of the hippocampus. As Elliot Smith has pointed out in various publications, the atrophy of the supracallosal hippocampus in Eutherians is generally to be ascribed to the pressure exercised by the growing corpus callosum. In the present instance, however, the corpus callosum is exposed to the same influence which also leads to the atrophy of the indusium. In discussing the factors concerned in the formation of the typical hippocampal figure of Mammals, Obenchain enumerates the following: external pressure, internal pressure, and neuro-biotactic influences. Of the former, downward pressure of the neopallium can be excluded in the present case, for here it is the neopallium which has clearly been displaced by the growth of the hippocampus. Internal pressure and neuro-biotactic influences must be assumed to be the main operating factors if a mechanical explanation of the hippocampal figure in *Macroscelides* is sought.

### *The Optic Thalamus.*

No attempt has been made here to identify and homologise the numerous collections of cells which go to make up the thalamus. Malone (10) has pointed out how widely variable the structure of the thalamus is in different mammals (with the exception of the hypothalamic region) and how impossible it is to homologise the component nuclei without the study of a closely-graded comparative series of brains. He also emphasises the arbitrary nature of attempting to subdivide the thalamus into "nuclei" by reference to the medullary laminae which lie in the substance of the thalamus rather than by a study of the characters of the nerve cells which form definite homogeneous groups. The general proportions of the thalamus of *Macroscelides* can be readily seen from the transverse sections through the brain figured in Plates I and II. One of the outstanding features is the bulk of the optic tract. It will be seen that a large proportion of the fibres of this tract terminates in the anterior corpus quadrigeminum. The lateral geniculate body is distinct though not conspicuously large in relation to the size of the optic tract. A close study of this nucleus shows that it consists of two distinct parts, separated by a medullary lamina, a small dorsal portion (*C.G.L.* (*d.*)) which is absent altogether at the rostral extremity of the nucleus and becomes larger at the caudal extremity, and a ventral portion (*C.G.L.* (*v.*)) which comprises by far the greater part of the nucleus but is absent in the sections through the caudal extremity. The ventral nucleus is formed of small cells fairly closely packed together. On its lateral aspect it is bounded by the optic tract from which it receives numerous fibres. From its medial border medullated fibres emerge and collect together to form a large part of the ventral medullary lamina (*L.M.V.*). The dorsal nucleus is formed of cells which are larger than those of the ventral nucleus, especially posteriorly, and which are much less closely packed. Moreover no fibres emerge from it to pass into the ventral region of the thalamus. There seems to be little doubt that these two nuclei correspond to the dorsal (pars magnocellularis) and ventral (pars parvicellularis) nuclei found generally in the lateral geniculate body of mammals (Kappers, Winkler, Minkowski, Woollard) of which it is believed that the dorsal nucleus is related to the optic radiations and the area striata of the neopallium, while the ventral nucleus is associated with the mid-brain and is concerned rather with mid-brain visual reflexes. It is to be expected therefore that the ventral nucleus should be so large in *Macroscelides*, in which the anterior corpus quadrigeminum is remarkably developed, while the small size and the feeble differentiation of the dorsal nucleus is correlated with the poorly differentiated area striata of the cortex.

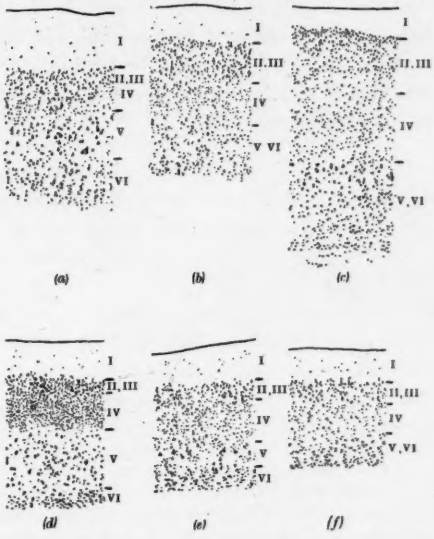
The medial geniculate body (*C.G.M.*) forms a conspicuous elevation immediately caudo-ventral to the lateral geniculate body. It is, however, much smaller than the latter, and shows no differentiation in its structure.

### *The Neopallium.*

The combined method of staining with Weigert-Pal and neutral red was sufficiently successful in the present instance to allow a complete study of the lamination of the cortex to be made, as a result of which it has been possible to indicate several distinct cortical areas which can be separated by reference to their particular and characteristic structure. Some of these areas are sharply limited at their margins, while others pass so gradually into the neighbouring areas that their boundaries can only be fixed very approximately. As is naturally to be expected in a primitive brain of this kind, cortical differentiation is by no means so perfect as it is in many mammalian brains, and this lack of differentiation is very obvious by comparison with the brain of *Tupaia* (3) and, to a much lesser degree, with that of *Ptilocercus* (4). If sections of the neopallial cortex of the other Menotyphla are compared with those of *Macroscelides*, it will be seen that the latter is generally poorly developed. The cortex is thin, not very densely packed with cells, and the supragranular layers are relatively shallow. In the temporal area, the enlarged hippocampus has stretched out the cortex into a thin atrophic-looking layer, and the anomalous development of this structure has also led to a considerable dislocation of the cortical areas from the positions in which they are usually found in mammalian brains. It will be convenient to describe separately the different cortical areas which can be distinguished in this brain.

*Area retrosplenialis granularis* (text-figs. 8 (*d*) and 9, *H* and *K*). This area may be described first because of its highly distinctive appearance. It can be subdivided into two parts, area *H*, which appears to correspond to areas 29 *a*, 29 *b*, 29 *c*, and 29 *d*, of Brodmann (1), and area *K*, which evidently corresponds either to his area 29 *e* or 27, area presubicularis These areas are characterised by the astonishing development of the lamina granularis interna. The small round and deeply-staining cells which form this layer are closely packed together, sometimes disposed in vertical or horizontal rows, to form a very conspicuous band. It is rendered still more conspicuous by the presence in this layer of fine interlacing myelinated fibres, which represent a highly developed outer line of Baillarger. The lamina zonalis is of moderate width, broader over the mesial part of the area than over the lateral. The lamina pyramidalis is very narrow and contains very small pyramidal cells. The lamina ganglionaris is wide and contains large pyramidal and polygonal cells scattered rather sparsely. The sixth layer is narrow, and the cells in it are rather crowded and flattened in a horizontal direction. This area corresponds almost precisely in its structure with the retrosplenial area of the rabbit as figured and described by Brodmann and Winkler and Potter (17). It is also figured by Brodmann (1) in *Pteropus*, *Lemur* and the kangaroo, by Watson (16) in *Erinaceus*, *Talpa* and *Sorex* (this author's specialised postero-mesial cortex), by Gray (6) in *Didelphys*, etc., and I have studied it in *Tupaia* and *Ptilocercus*, but in none of these animals is the granular layer so con-

spicuously developed as it is in Rodents (*Lepus*, *Mus*, *Cavia* (1), (12)) and *Macroscelides*. Area *K* shows a marked increase in the development of the internal granular layer, a broad lamina zonalis, the practical disappearance of layers 2 and 3, and a great reduction of the infragranular layers which no longer contain large deeply-stained cells. These two areas may be regarded as together forming the *area retrosplenialis*. The extent of this area in *Macroscelides* is no less striking than its structural differentiation. It reaches forward above the corpus callosum as far as the anterior quarter of this commissure. Up to this level, also, it extends over the dorso-medial border of the hemisphere

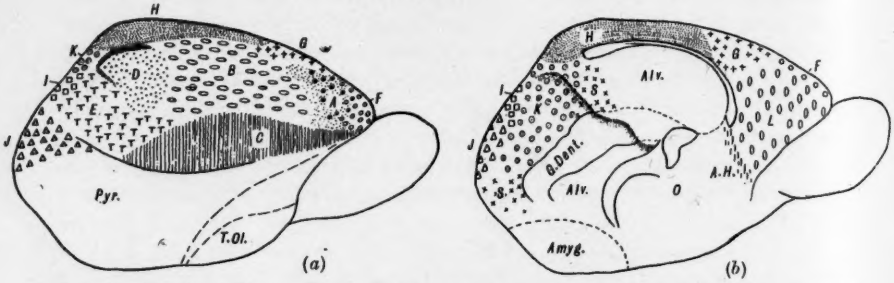



Text-fig. 8. Cortical areas of *Macroscelides*. Traced with a projectoscope. (*a*) Sensorimotor area. (*b*) Parietal area. (*c*) Insular area. (*d*) Retrosplenial area. (*e*) Striate area. (*f*) Temporal area. (The figures refer to Brodmann's system of lamination.)

on to the dorso-lateral surface of the brain. Here the lateral border, which is very sharply defined, is bounded by a shallow furrow on the surface which is reflected in a local thickening of the lamina zonalis and a corresponding indentation of the pyramidal layer of cells (Plate II, fig. 19, *I.S.*). This subzonal sulcus is also represented in the rabbit's brain in Winkler and Potter's figures where these authors label it the *fissura sagittalis lateralis*. From its relation to the retrosplenial area, however, it is clear that this sulcus represents the splenial element of the intercalary complex pushed over on to the lateral surface of the hemisphere by the extension of the retrosplenial area, and also in *Macroscelides* by the displacement of the corpus callosum. This was recognised by Elliot Smith (14) in the brain of *Tragulus*, in which

a similar condition is to be found (see also Brodmann (1), p. 215). In almost all mammals, the retrosplenial cortex is limited to a small area immediately behind and below the splenium of the corpus callosum. Its great extent in *Macroscelides* is, however, not entirely unique, for it is to a considerable degree approached by the condition found in Rodents and *Tragulus*.

*Area retrosplenialis agranularis* (text-fig. 9, *I*). This name is applied to a small but well-differentiated area lying on the posterior border of the cerebrum between the posterior piriform area and the presubicular area. It seems to correspond to the area of this name (area 30) of Brodmann. The lamina zonalis is broad, the pyramidal layer is well developed and consists of relatively large polygonal cells which hardly vary in size at different levels and stain very lightly as compared with the pyramids in other cortical areas, small granules seem to be quite absent, and the lamination is very indistinct. The margins of this small localised area are peculiarly abrupt, especially where it borders on the presubicular area.




Text-fig. 9. Brain of *Macroscelides* from (*a*) the lateral aspect, and (*b*) the medial aspect, mapped out to show the extent of the various cortical areas described. *A*. Sensorimotor area. *B*. Parietal area. *C*. Insular area. *D*. Striate area. *E*. Temporal area. *F*. Frontal area. *G*. Posterior cingular area. *H*. Retrosplenial area. *I*. Area retrosplenialis agranularis. *J*. Posterior piriform area. *K*. Presubicular area. *L*. Anterior cingular area. *A.H*. Anterior hippocampus. *Alv*. Alveus. *G.Dent*. Gyrus dentatus. *Amyg*. Amygdala. *S*. Subicular cortex. *Pyr*. Piriform lobe. *T.Ol*. Tuberculum olfactorium. ×5.

The *subicular area* (text-fig. 9, *S*) has the usual characteristic structure, a broad zonal layer and a single broad layer of medium pyramids rather widely scattered. Most of the subiculum is buried from the surface in the *fissura hippocampi*, but portions appear on the medial aspect of the brain in the two regions indicated on the map.

*The sensorimotor area* (text-figs. 9, *A*, and 8 (*a*)). This name is applied to a small area at the anterior end of the dorso-lateral surface of the cerebrum. It is characterised by the presence in the lamina ganglionaris of a layer of large broad pyramidal cells which stain very deeply, and a well-marked band of fine myelinated fibres in the same lamina further adds to the distinctive nature of this cortical area. The lamina zonalis is broad, the pyramidal layer is relatively thin, and the lamina multiformis is moderately developed. The

internal granular layer is variably developed. It is poorly represented at the anterior extremity and along the mesial border of the area, while posteriorly and laterally it becomes more conspicuous and even well developed. This area seems to combine the features of the motor and sensory (precentral and postcentral) areas found in most mammalian brains, and it seems probable that the former is represented by the mesial and anterior (relatively agranular) and the latter by the lateral and caudal (relatively granular) part of this common sensorimotor area. It must be emphasised that the term "sensorimotor" is here applied in a tentative manner only, for Gray found that, in the opossum, the electrically excitable area of the brain did not accurately correspond to the agranular area of the cortex which might be regarded as the area precentralis on the basis of histological evidence.

The *frontal area* (text-fig. 9, *F*) is confined to the rostral extremity of the cerebral hemisphere, and is characterised by a deep pyramidal layer, a complete absence of small granules, the absence of large pyramidal cells in the infragranular layers and imperfect lamination.

The *parietal area* (text-figs. 8 (*b*) and 9, *B*) shows a pyramidal layer rather broader and more regular than in other areas. The inner granular layer is well developed, and there is a lack of large pyramids in the lamina ganglionaris. The boundary line between this area and the two areas next to be described is very indistinct.

The *visual area* (text-figs. 8 (*e*) and 9, *D*) was identified by the broad layer of granules forming lamina IV, the presence of darkly-staining pyramidal cells with broad bases in the lamina ganglionaris (evidently representing the cells of Meynert), the narrow lamina multiformis and the narrow pyramidal layer. It is regarded as the visuosensory area solely by comparing its structure and relative position on the surface of the brain with these features of the visual area found in many other mammalian brains. No trace of the stria of Gennari was found in these specimens although they were stained by the Weigert-Pal method, and it may be assumed to be absent. The anterior and ventral boundaries of this area are very ill-defined. Above, it is separated from the retrosplenial area by a narrow band of cortex in which the inner granular layer is thinner. This band of cortex may be regarded as the peristriate area and it closely resembles this area which is figured by Gray for the opossum (6).

The *temporal area* can only be recognised by its negative characters. The pyramid layer is not well developed, the inner granular layer is of moderate thickness, and there are no conspicuous pyramids in the infragranular layers. As has been already indicated, this area grades insensibly into the parietal and visual areas, so that the junction of these three areas cannot be fixed with any precision. It is clear, therefore, that the boundaries of these three areas as represented on the accompanying map are only approximate. The temporal cortex is relatively thin throughout its extent, consequent on the pressure which appears to be exerted on it by the subjacent hippocampus.

*The insular area* (text-figs. 8 (*c*) and 9, *C*). This cortical area is characterised by its great depth and rather imperfect lamination. The moderately developed pyramidal layer, which is apt to be rather irregular, is followed by a broad internal granular layer. The infragranular layers are also broad and imperfectly divided into lamina ganglionaris and lamina multiformis. The former contains many medium-sized pale pyramidal cells. The claustrum appears to be represented by a clump of darkly-staining cells lying deep to the rhinal fissure, so that it comes into relation superficially with the ventral margin of the insular cortex above and the dorsal margin of the piriform cortex below. There is at least no other separate cell mass which could be regarded as the claustrum.

*The cingular area* (text-fig. 9, *G* and *L*). This area is situated on the mesial surface of the hemisphere in front of the area retrosplenialis. The posterior part consists of rather poorly stratified cortex with an inner granular layer. This part, of small extent, reaches over to the dorso-lateral surface of the brain, and would appear to correspond to Brodmann's area 23. The anterior part of the cingular area is agranular, extends down over the mesial surface of the brain in front of the corpus callosum and probably corresponds to Brodmann's area 24.

*General.* The displacement of the cortical areas from the usual positions in which they are found in the mammalian cerebrum by the enlarged subsplenial flexure of the hippocampus has already been noted. The charts indicate sufficiently clearly the lateral displacement of the retrosplenial area and the posterior part of the cingular area on to the dorsal aspect of the brain. With this is associated a lateral displacement of the visual area which does not occupy the dorso-caudal pole of the hemisphere in *Macroscelides* as it does in mammals generally. A similar position of the corresponding area is to be noted in Rodents and *Tragulus*.

The relatively great extent and the advanced degree of differentiation of the retrosplenial, subicular and presubicular areas stand in marked contrast to the ill-defined nature of the visual, temporal, sensorimotor and parietal areas. This contrast is undoubtedly associated with the conspicuous development of the hippocampal cortex, for the retrosplenial and associated areas are to be regarded as annectant between the old and new pallium. The resemblance between the retrosplenial region of the cortex in *Macroscelides* and Rodents is certainly striking, though its significance is obscure. It may be noted that the area retrosplenialis agranularis, which though of limited extent is so clearly differentiated in *Macroscelides*, is said by Brodmann to be absent in Rodents.

## DISCUSSION

The brain of the Macroscelididae is clearly a macrosmatic brain, but not remarkably so. Thus, comparing the brain with those of *Erinaceus* and *Talpa*, two lowly insectivores, the olfactory bulbs, the tuberculum olfactorium, and the piriform lobe are not so proportionately large. The general resemblance

in the contour of the cerebrum to that of the mole has been noted by Elliot Smith. In the elephant shrew the antero-posterior shortening and the transverse width of the hemispheres which are so characteristic in the mole are not shown to the same degree. In the mole, also, the optic nerves are reduced to fine threads, while in the elephant shrew they are nerves of conspicuous size. This is correlated with a marked development of some of the visual centres of the brain and especially the anterior corpora quadrigemina which reach such dimensions that they are exposed on the dorsal aspect of the undissected brain. Compared with the brain of the mole the impression is gained that the exposure of the corpora quadrigemina in this manner is due rather to their own unusual development than to a relatively feeble development of the cerebral hemispheres. As already mentioned, the primary and secondary olfactory areas are well developed but not in any way to an unusual degree. In contrast to this, the relatively large size and differentiation of the amygdaloid complex and the enormous mass of the hippocampal formation stand out as two of the most striking features of this brain. The great expansion of the subcallosal portion of the ammon's horn has led to a distortion of the corpus callosum and the neopallium, and has displaced the septal formation altogether from the interval between the hippocampal and callosal commissures. It has likewise led to an extreme atrophy of the supracallosal portion of the hippocampus. This immense and seemingly bizarre development of the hippocampus is out of all proportion to the development of the primary and secondary olfactory areas, and this fact serves further to confirm what has been suggested by Elliot Smith's remark that the hippocampus does not diminish in size *pari passu* with the diminishing of the olfactory bulb like the tuberculum olfactorium and the piriform lobe, and by the observations of other authors, namely, that the hippocampus may well be concerned with the elaboration of other than purely olfactory stimuli. It does not follow from this, of course, that the hippocampus is not an organ which is predominantly associated with olfactory stimuli, but it indicates that it is at least not so closely related to the primary olfactory regions as are the olfactory tubercle and the piriform lobe. In connection with the piriform lobe, it may be noted that the specialised area piriformis posterior, which is regarded as being entirely concerned with functions of an associational nature, is not developed to any marked extent. Correlated with the size of the hippocampus is the size of the hippocampal commissure which in cross-section is triangular or crescent-shaped, and thus closely resembles the typical appearance of the metatheroid psalterium. It may be doubted, however, whether this appearance can be regarded as indicative of marsupial affinities. The shape of the cut commissure would seem to be the direct result of the large size of the commissure coupled with the pressure of the superjacent hypertrophied subsplenial hippocampus which evidently exerts a pressure downwards and forwards between the corpus callosum and the psalterium leading to a bending downward and forward of

the dorsal part of the latter commissure. A comparison between the brains of *Macroscelides* and *Elephantulus* adds some force to this suggestion, for in the former, in which the hypertrophy of the subsplenial portion of the hippocampus is more exaggerated, the psalterium is distinctly more crescentic and metatheroid in appearance.

In regard to the amygdaloid complex, the most notable features are the clear differentiation of the various nuclei and the predominating size and organisation of the lateral nucleus. The significance of the latter is not known. Johnston (8) notes that it appears to be least intimately related to the other parts of the amygdala, and that it does not seem to share in the distribution of stria terminalis bundles. Johnston's comparative studies of the amygdala do not indicate that there is any relation between the development of the hippocampus and the relative size of the lateral amygdaloid nucleus, and in his description of the brain of *Orycteropus*, in which the hippocampus is described as being a massive structure, Woollard does not note that the lateral amygdaloid nucleus is unusually large. The basal amygdaloid nucleus is conspicuously marked out by the large size of its component cells, but this nucleus is not so large relatively as it is, for instance, in the brains of *Tupaia* and *Ptilocercus*, two other menotyphlous insectivores.

The shape of the corpus callosum differs notably in *Macroscelides* and *Elephantulus* and this difference, again, allows us to conjecture how far the appearance of this commissure is correlated with mechanical influences exerted by the hypertrophied hippocampus. In the former species the larger subcallosal hippocampus has pushed the corpus callosum further dorsally, so that the mesial surface of the cerebral cortex is reduced to a narrow strip, and at the same time the commissure has evidently been more elongated and thinned as the result of the mechanical pressure. In *Elephantulus* these effects have been produced to a much less marked degree, and the corpus callosum is shorter and thicker. It would appear, therefore, that the length of the commissure is at least in part resultant from the development of the hippocampus. The pronounced curved genu is likewise produced by a moulding of the commissure around the rostral extremity of the enlarged hippocampus. It seems possible also that the presence of the splenial kinking of the corpus callosum may be partly associated with the subsplenial flexure of the hippocampus. It is more conspicuous in *Macroscelides* than in *Elephantulus*, and I have noted in the study of the brains of *Tupaia* and *Ptilocercus* (in which the brains are very similar in external contour) that in the latter where the corpus callosum shows a well-marked splenium there is also a conspicuous subsplenial flexure of the hippocampal formation, whereas in the former there is no such hippocampal flexure and the corpus callosum has no proper splenium. But even if these features of the corpus callosum are effected by such mechanical influences, they are only produced by virtue of the relatively large size of the commissure. Even were the distorting influences of the hippocampus to be removed, the corpus callosum would remain an astonish-

ingly large commissure for a primitive brain. It is difficult to advance an adequate reason in explanation of this feature. The neopallium is poorly developed, and is not only limited in its surface area but is also considerably thinned out by pressure of the hippocampal formation. On the other hand, the entral commissure is correspondingly small, and appears from the sections to be formed to a greater extent by the intermediate olfactory tract and by fibres of the stria terminalis than by fibres from the external capsule. The idea suggests itself that the growing hippocampus has exerted such pressure laterally against the pallium and the corona radiata (and the existence of such pressure is indicated by the thinning out of the pallium in this region) that the commissural fibres from the greater part of the neopallium are prevented from taking the phylogenetically older path through the ventral commissure and, instead, cross over through the corpus callosum. One is tempted to go further and to suggest that the pressure of a rapidly enlarging hippocampal formation originating in this way may have decided the initial appearance of a callosal commissure in the evolutionary development of eutherian mammals from metatherian forerunners. However this may be, such a large corpus callosum as is found in the Macroscelididae, coupled with a diminutive ventral commissure, is to be regarded as a progressive trait, and its association here with such a poorly developed neopallium renders the difficult problem of the significance of the callosal commissure still more obscure.

The large size of the optic nerves is reflected in the great development of the anterior corpus quadrigeminum (already referred to) and in the differentiation of the lateral geniculate body. The fact that this body is formed mainly by the ventral element and that the dorsal element is so relatively insignificant is correlated with the large size of the anterior corpus quadrigeminum and the undifferentiated condition and small extent of the area striata of the cortex. Ganser (5) has noted the very small size of the lateral geniculate body in the mole's brain, and he found much difficulty in differentiating it from the mass of the optic thalamus. A similar lack of differentiation is to be found in the hedgehog's brain. The other extreme among insectivores is to be found in the brain of *Tupaia*, in which the optic nerves are large and the striate cortex elaborately differentiated. In this brain, the ventral nucleus is large, in association with the great size of the anterior corpora quadrigemina (Woollard (19)), but what appears to be more significant is the large size of the dorsal element, the large size of the individual cells of which it is composed, and its conspicuous lamination. In *Ptilocercus*, in association with the moderate size of the optic nerves, the lateral geniculate body is smaller. The ventral nucleus is absolutely and relatively smaller than in *Tupaia*, and this is evidently correlated with the much smaller size of the anterior corpus quadrigeminum. The dorsal nucleus, on the other hand, although larger relatively to the ventral nucleus than is the case in *Tupaia* for the reason just mentioned, is not so large relatively to the brain as a whole, and not nearly so conspicuously organised. This series of insectivore brains affords

an excellent illustration of the correlation between the development of the optic nerves, the anterior corpus quadrigeminum, the lateral geniculate body, and the area striata of the cortex.

The neopallium is characterised by its general thinness, the relative poverty of its cell content, the poor development of the pyramidal layer and, except in certain regions, its lack of differentiation. On the other hand, the retrosplenial areas show a degree of differentiation and a surface extent which are quite remarkable. The significance of this feature, however, is by no means apparent. It may be surmised that there is some association between the development of this cortical area and the development of the subsplenial portion of the hippocampus. But the retrosplenial area is almost as well developed in many rodents, and in *Tragulus*, in which the subsplenial part of the hippocampus, even if conspicuous, is not to be compared with the condition found in *Macroscelides*.

It is disappointing to find that the anatomical details of the brain seem to be of little use in the determination of the taxonomic position of the Macroscelididae. Indeed, a comparison with the brains of the other family of the Menotyphla, the Tupaiidae, is even a little disturbing, for it would be difficult to find brains of small insectivorous mammals of similar size which show more divergent characteristics. *Tupaia* is a diurnal, arboreal mammal, with well-developed eyes and rudimentary ears, and shows evidence of a reduction of the olfactory regions of the brain. The anterior corpus quadrigeminum is very large, and the posterior very small. The lateral geniculate body shows an advanced degree of development of the dorsal nucleus. The visual cortex is highly differentiated and extends on the medial surface of the hemisphere right down to the dorsal surface of the corpus callosum. Reduction of the hippocampal formation is indicated by the complete absence of any subsplenial flexure. The piriform lobe is relatively diminished, and is largely pushed down from the lateral aspect of the cerebrum by the extension downward of the temporal lobe of the neopallium. The neopallial cortex shows a conspicuous differentiation.

*Ptilocercus* is a nocturnal arboreal mammal with well-developed external ears. Its brain is distinctly more primitive than that of *Tupaia*. The olfactory bulbs are larger, the piriform lobe relatively bigger, and there is a well-marked subsplenial hippocampal flexure. The anterior corpus quadrigeminum is small, while the posterior is more prominent. The moderate development of the lateral geniculate body contrasts with the size of the medial geniculate body. The visual cortex is not well differentiated and appears to be of small extent. The temporal area of the cortex, however, shows a more pronounced lamination. In both these tree shrews, the fornix commissure is of moderate size, and bears no resemblance to that of the elephant shrew. In the size of the corpus callosum there is certainly a point of similarity between the Macroscelididae and the Tupaiidae, and in this feature there is perhaps an argument for separating them as the Menotyphla from the other members of the Insectivora.

But it seems doubtful whether this argument is really valid, especially as Elliot Smith (14) has recorded that *Chrysochloris* has an "extraordinary elongation" of the corpus callosum. It must be admitted, indeed, that the cerebral anatomy supplies no justification for associating the Macroscelididae with the Tupaiidae. On the contrary, it suggests that the two families represent widely divergent forms. Carlsson (2), in 1909, reviewed the question of the relationship of the Macroscelididae to the other Insectivora, and concludes that, in the absence of fossil remains to indicate otherwise, the general anatomical evidence suggests that they branched off from the ancient Erinaceidae, inheriting from the latter a multitude of primitive characters. The evidence of cerebral anatomy is quite compatible with this hypothesis.

## SUMMARY

1. The brain in the Macroscelididae is a primitive, macrosmatic brain in which an unusual development of the subsplenial portion of the hippocampus has led to certain distortions and displacements of other cerebral structures.

2. It is thought possible that this hippocampal hypertrophy may (at least in part) account for the unusual features of the cerebral commissures.

3. The amygdaloid complex of nuclei is conspicuously differentiated and the lateral amygdaloid nucleus is notable for its relatively large size.

4. The optic nerves and tracts are large, and this is correlated with a great development of the anterior corpus quadrigeminum (which as a result of its own size becomes exposed on the dorsal aspect of the undissected brain). The lateral geniculate body is likewise clearly differentiated from the rest of the optic thalamus, but by far the greater part of it is formed from the ventral nucleus, and, in conformity with the very small size of the dorsal nucleus, the *area striata* of the cortex is poorly differentiated and of relatively small extent.

5. The neopallium is, on the whole, poorly developed, appears to be largely thinned out by the pressure of the intraventricular portion of the hippocampus, and many of the cortical areas into which it can be subdivided can only be approximately delimited.

6. The retrosplenial areas of the cortex, on the contrary, are remarkably differentiated and their surface extent on the cerebral hemisphere is unusually great. Herein the Macroscelididae show a striking resemblance to the condition recorded in many rodents and in the primitive ungulate *Tragulus*.

7. In spite of the poor neopallial development, the corpus callosum is obtrusively large. No explanation can be offered for this association of a conspicuous callosal commissure with such a primitive brain.

8. As a result of this study and of a comparison with the brains of the Tupaiidae, there seems no adequate reason for associating the Macroscelididae with the Tupaiidae in a common group, the Menotyphla, at least on the basis of cerebral anatomy. On the contrary there seem to be good reasons for widely

separating the tree shrews from the elephant shrews in a natural system of classification.

9. The brain of the Macroscelididae may readily have been derived from the brain of a primitive Erinaceid in which a progressive and unique enlargement of the subsplenial hippocampus has produced certain very aberrant features.

10. This enlargement of the subsplenial hippocampus and its disturbing effects on other parts of the brain have progressed to a much greater degree in *Macroscelides* than in *Elephantulus*.

11. The marked difference between the brains of *Macroscelides* and *Elephantulus* justifies the separation of these forms into two distinct genera as originally proposed by Oldfield Thomas.

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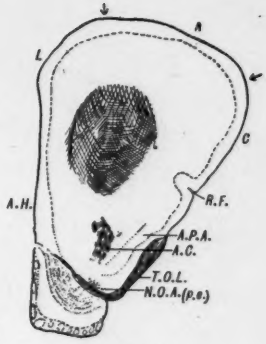
Fig. 10.

Fig. 11.

Fig. 12.

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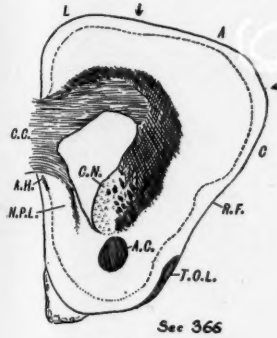


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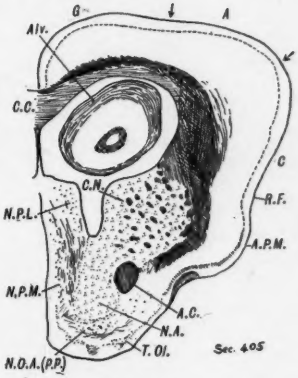


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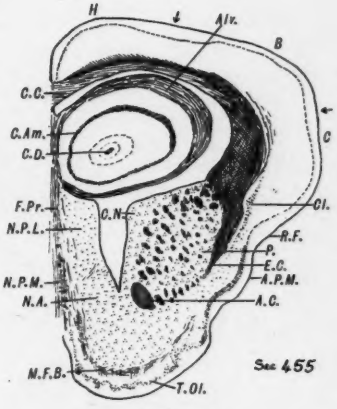


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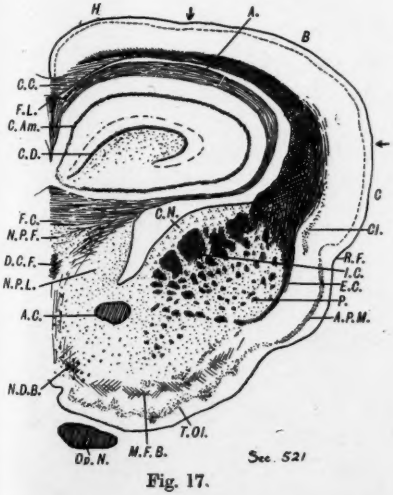


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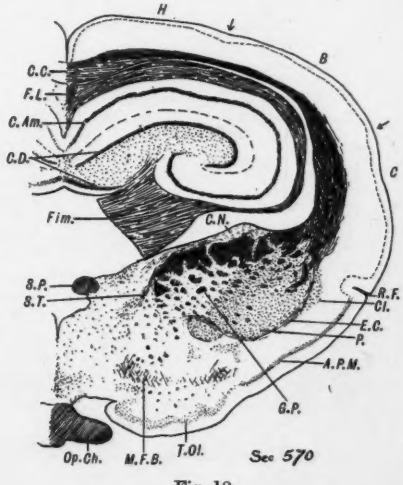


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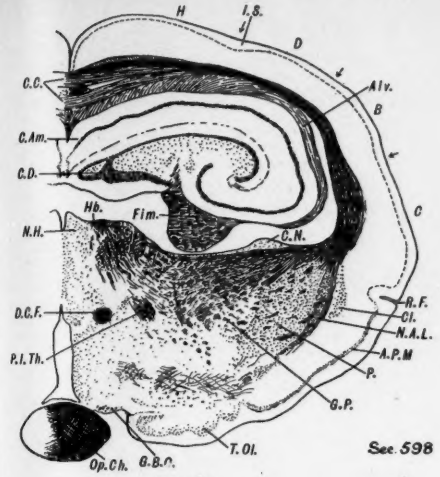


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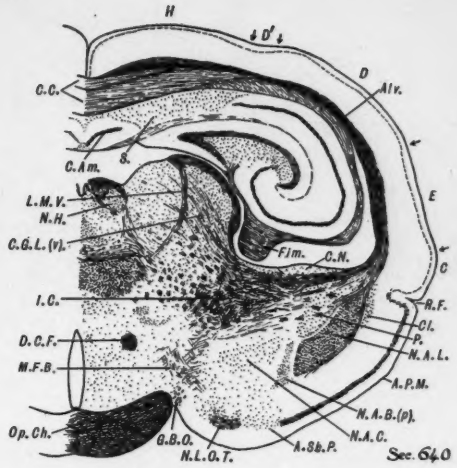


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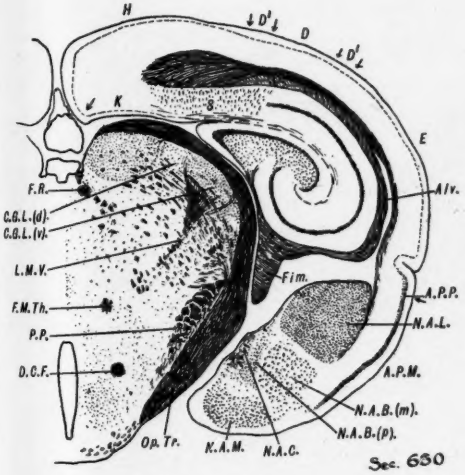


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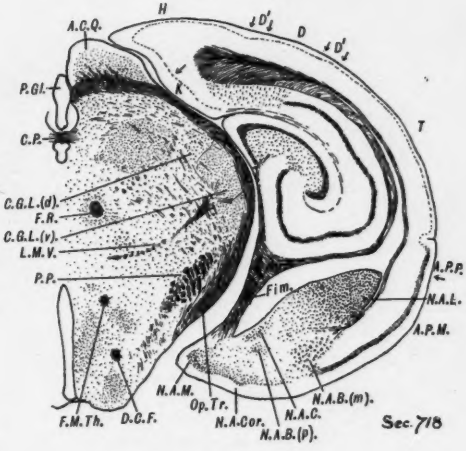


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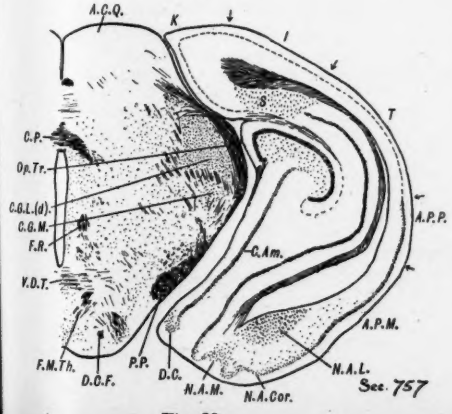


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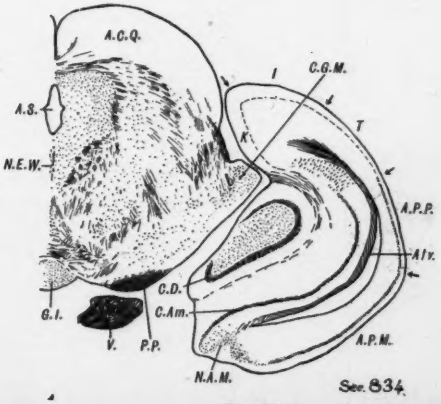


Fig. 24.

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## KEY TO ILLUSTRATIONS

| | |
|---|---|
| *A.* | Sensorimotor area of cortex |
| *Ac.B.* | Accessory bulb |
| *A.C.* | Anterior commissure |
| *A.C.Q.* | Anterior corpus quadrigeminum |
| *A.H.* | Anterior hippocampus |
| *Alv.* | Alveus |
| *A.P.A.* | Area piriformis anterior |
| *A.P.M.* | Area piriformis medius |
| *A.P.P.* | Area piriformis posterior |
| *A.S.* | Aqueduct of Sylvius |
| *A.Sb.P.* | Area subpiriformis |
| *B.* | Parietal area of cortex |
| *C.* | Insular area of cortex |
| *C.C.* | Corpus callosum |
| *C.D.* | Cortex dentatus |
| *C.G.L.* (*d.*). | Lateral geniculate body (dorsal nucleus) |
| *C.G.L.* (*v.*). | Lateral geniculate body (ventral nucleus) |
| *C.G.M.* | Medial geniculate body |
| *Cl.* | Claustrum |
| *C.N.* | Caudate nucleus |
| *C.P.* | Posterior commissure |
| *D.* | Area striata of the cortex |
| *D.C.F.* | Descending column of fornix |
| *E.* | Temporal area of the cortex |
| *E.C.* | External capsule |
| *F.* | Frontal area of the cortex |
| *F.C.* | Fornix commissure |
| *Fim.* | Fimbria |
| *F.L.* | Fornix longus |
| *F.M.Th.* | Fasc. mammillo-thalamicus |
| *F.Pr.* | Precommissural fornix |
| *F.R.* | Fasc. retroflexus |
| *G.* | Posterior cingular area of the cortex |
| *G.B.O.* | Ganglion basale opticum |
| *G.I.* | Ganglion interpedunculare |
| *G.P.* | Globus pallidus |
| *H.* | Area retrosplenialis granularis |
| *Hb.* | Habenula |
| *I.* | Area retrosplenialis agranularis |
| *I.C.* | Internal capsule |
| *I.S.* | Intercalary sulcus |
| *K.* | Retrosplenial area (29 *e*) or Area presubicularis |
| *L.* | Anterior cingular area of the cortex |
| *L.M.V.* | Lamina medullaris ventralis |
| *M.F.B.* | Medial fore-brain bundle |
| *N.A.* | Nucleus accumbens. |
| *N.A.B.* (*m.*) | Nucleus amygd. basalis (pars magnocell.) |
| *N.A.B.* (*p.*) | Nucleus amygd. basalis (pars parvicell.) |
| *N.A.C.* | Nucleus amygd. centralis |
| *N.A.Cor.* | Nucleus amygd. corticalis |
| *N.A.L.* | Nucleus amygd. lateralis |
| *N.A.M.* | Nucleus amygd. medialis |
| *N.D.B.* | Nucleus of the diagonal band |
| *Neo.* | Neopallium |
| *N.E.W.* | Nucleus of Edinger Westphal |
| *N.H.* | Nucleus habenulae |
| *N.L.O.T.* | Nucleus of lateral olfactory tract |
| *N.O.A.* | Anterior olfactory nucleus |
| *N.O.A.* (*p.e.*) | Anterior olfactory nucleus (pars externus) |
| *N.O.A.* (*p.p.*) | Anterior olfactory nucleus (pars posterior) |
| *N.P.F.* | Nucleus proprius fornicis |
| *N.P.L.* | Nucleus parolfactorius lateralis |
| *N.P.M.* | Nucleus parolfactorius medialis |
| *Op.Ch.* | Optic chiasma |
| *Op.N.* | Optic nerve |
| *Op.Tr.* | Optic tract |
| *P.* | Putamen |
| *P.Gl.* | Pineal gland |
| *P.I.Th.* | Pedunc. inferior thalami |
| *P.P.* | Pes pedunculi |
| *R.F.* | Rhinal fissure |
| *S.* | Subiculum |
| *S.P.* | Stria pinealis |
| *S.T.* | Stria terminalis |
| *Str.G.* | Stratum glomerulosum |
| *Str.Gr.* | Stratum granulare |
| *Str.Plex.* | Stratum plexiforme |
| *T.Ol.* | Tuberculum olfactorium |
| *T.O.I.* | Intermediate olfactory tract |
| *T.O.L.* | Lateral olfactory tract |
| *V.* | Trigeminal nerve |
| *V.D.T.* | Ventral decussation of the tegmentum |

## EXPLANATION OF PLATES

Plates I and II, figs. 10 to 24. Transverse sections through the brain of *Macroscelides*, traced with a projectoscope. $\times 8\frac{1}{3}$.

# EPICRITIC AND DYSCRITIC SYSTEMS IN A PRIMITIVE PRIMATE

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The application of Sir Henry Head's principles to comparative neurology has been already made by Brouwer and others, and more recently by Sir John Parsons. This has not only been of advantage to comparative anatomy but it has also furnished a new confirmation of Head's conclusions. For the present the evaluation of the anatomy of the nervous system in accordance with the dual organisation of Head must be largely qualitative. It is not impossible that later it may be applied quantitatively and so yield results of great precision. However, factors of body surface and area, the inverse relation of the size of the brain to the size of the animal in the same species, the varying arrangement of certain tracts in the central nervous system, render quantitative estimation at the moment of approximate value only.

The term epicritic is used to imply those aspects of sensation which form the basis of discrimination. The anatomical criterion of these is that they involve the cerebral cortex. Sir John Parsons's term dyscritic for the non-discriminative aspect of sensation is chosen in preference to others that have been used, such as protopathic, vital, nociceptive, etc., since it expresses the antithesis to epicritic more neatly. Since an analysis of systems, to which Head's interpretation can be obviously applied, exhibits very clearly the predictable anatomical arrangement, the same interpretation can be extended to other systems which have usually not been so regarded. Indeed it seems hard to escape the belief that all the elaborations of nuclear masses, e.g. cerebellar, olivary, red nucleus, etc., are changes from a purely dyscritic to an epicritic type. In the same way the change on the efferent side from a crude massive response to a finely graded phasic movement may be similarly regarded.

The primitive primate used in this study is *Tarsius spectrum*. For the *Tarsius* material I am indebted to Prof. Elliot Smith. It is a pleasure to express again my thanks to him.

The position which this animal occupies in Primate evolution makes it of especial interest to the human anatomist. *Hapale*, with which I have compared my material, was chosen for this purpose for a number of reasons. Genetically the Platyrrhines arose from the Tarsioids. *Hapale* is comparable in size and represents a definitely higher level of neural organisation. Earlier studies of the Lemuroidea have led me to believe that on neurological grounds

these have developed special features which render them less instructive than *Hapale*.

## POSTERIOR COLUMNS

It directly follows from the work of Head that the number of fibres in the posterior columns must bear a direct relation to the level of neurological organisation of the animal. In seeking a measure of the development of these columns Brouwer expressed the size of the posterior column as a ratio to the rest of the white substance of the cord at the same level. Kappers used the ratio of the posterior columns to the grey matter in the cervical region of the cord and also compared the increase in these columns in the cervical region to their amount in the lumbar region. As has already been mentioned the actual figures are not of much moment, for there are several disturbing factors. But the lists prepared by Kappers and Brouwer do bring out the great increase in these columns in the higher Primates and man. In measuring the proportions of these columns in *Tarsius* to the remaining white matter in the cervical region the result obtained is the relatively high figure of 20 per cent. The same ratio in *Hapale* is about 25 per cent. This may be regarded as a quite high level of development in *Tarsius*, since it is somewhat higher than the figures allotted to other small mammals of the Carnivore, Rodent, and Marsupial Orders. If the figures for *Tarsius* and *Hapale* could be corrected for differences in size the figures would approximate more closely.

The nuclei of Goll and Burdach vary in their size and extent with the development of the posterior columns. In the monkeys the nucleus of Goll is relatively larger than in man. The nuclei of Goll and Burdach become connected together by grey matter and exhibit a considerable degree of lamination.

Bishop's nucleus lies as a slender medial column on either side of the posterior median fissure and is probably connected with the tail. This nucleus in *Tarsius* is a slender accumulation of cells situated spinalwards. It is soon lost as a separate nucleus. The nuclei of Goll and Burdach become continuous and are of equal extent in *Tarsius*. The cells in both form a continued series which becomes very markedly convoluted.

## THE TRIGEMINUS

Brouwer and Stopford have definitely shown that the fifth nerve exhibits in the central connections of its fibres a segregation of epicritic from dyscritic sensibility. The tractus spinalis contains those fibres which carry the impulses of protopathic and thermal stimuli as well as the impulses arising from crude contact, while the chief sensory nucleus receives the fibres concerned with epicritic sensibility. Both nuclei show localisation. In the chief sensory nucleus Brouwer has been able to distinguish the cells belonging to the ophthalmic division. In the tractus spinalis the mandibular, the maxillary and the ophthalmic, in so far as they carry impulses of the dyscritic type, are represented in this order in a cranio-caudal direction.

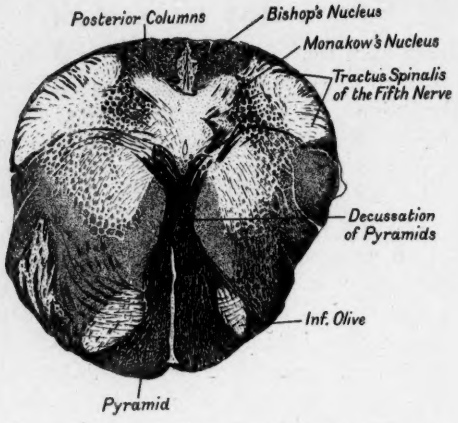


Fig. 1. Transverse section. Weigert-Pal. Brain stem of *Tarsius*. × 12.

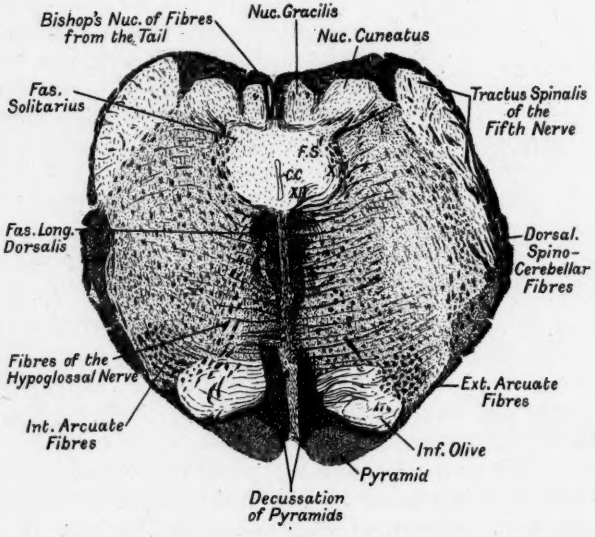


Fig. 2. Transverse section. Weigert-Pal. *Tarsius*. × 12

If the tractus trigeminus spinalis be compared with the extent of the posterior columns at the level where the nuclei of Goll and Burdach are well developed, it would appear that in *Echidna*, for instance, the fifth root is enormous and far exceeds the nuclei of the posterior columns. In the rabbit it is much smaller than in *Echidna* though still larger than the posterior column nuclei. In the cat, however, the tractus spinalis is reduced in volume and is not so large as the posterior columns. In *Tarsius* the condition more nearly resembles that of the rabbit and the tractus spinalis seems very large and is definitely in excess of the posterior columns. In *Hapale* the area of the spinal portion of the fifth is less than that of the posterior columns.

The mesencephalic root does not appear to extend very far cranialwards. It is usually at the level of the third nerve nucleus that it is best developed, but in *Tarsius* this would seem not to be the case since it is not very apparent at this level. The extension cranialwards of the mesencephalic root is more marked in higher members of the Primates. The motor and chief sensory nuclei are easily recognised in *Tarsius*. By comparing their respective sizes some idea can be obtained of the value of the epicritic element. In the rabbit the motor nucleus appears to exceed in size the chief sensory nucleus. In the cat the reverse is the case, and the same is true for *Hapale*. In *Tarsius* there is evidence of progress in this respect also, since the chief sensory nucleus is larger than the motor nucleus.

## THALAMUS

Sachs, as the result of experimental and comparative investigations, distinguished the following nuclei in the thalamus:

(1) The nucleus anterius or nucleus dorsalis magnocellularis. This is well developed in *Tarsius* and as in all the lemurs and *Hapale* it does not reach the surface since it is covered by the nucleus disseminatus. It is said that in the anthropoids the anterior nucleus is exposed on the surface. It has been a matter of controversy as to whether this nucleus contributes fibres to the thalamic radiation, or whether, as Sachs contends, it gives fibres only to the striatum. The sections studied leave no doubt that fibres from this nucleus and also from the median nucleus can be traced into the striatum. It is more difficult to exclude the possibility that they also give off fibres to the thalamic radiation, but the sections afford no clear evidence that they do.

(2) The median nucleus is well developed. Kappers is of the opinion that this area is related to the trigeminus and concerned in oral sensibility. No evidence for or against this has been obtained from a study of the sections. This area of the thalamus is apparently of the same extent relatively in *Tarsius* as in the lemurs and *Hapale*.

(3) The lateral nucleus was subdivided by Sachs into a dorsal and a lateral portion. The latter can be further divided into a lateral ventral internal, and

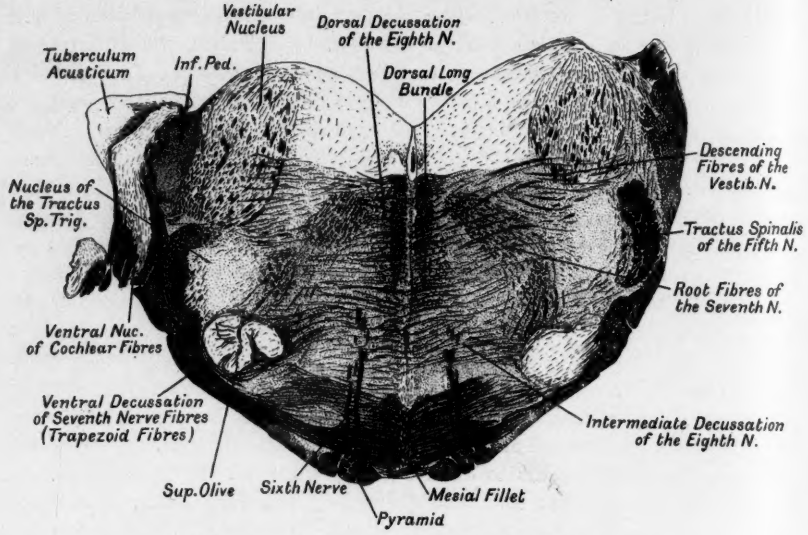
Vestibular Nucleus
Dorsal Decussation of the Eighth N.
Tuberculum Acusticum
Inf. Ped.
Dorsal Long Bundle
Descending Fibres of the Vestib. N.
Nucleus of the Tractus Sp. Trig.
Tractus Spinalis of the Fifth N.
Root Fibres of the Seventh N.
Ventral Nuc. of Cochlear Fibres
Ventral Decussation of Seventh Nerve Fibres (Trapezoid Fibres)
Intermediate Decussation of the Eighth N.
Sup. Olive
Sixth Nerve
Mesial Fillet
Pyramid

Fig. 3. Transverse section. Weigert-Pal. *Tarsius.* × 12.

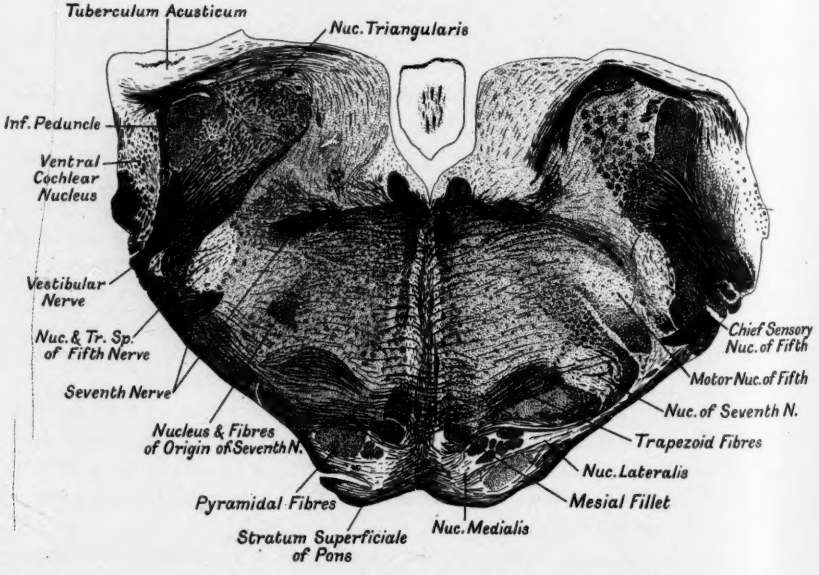


Fig. 4. Transverse section. Weigert-Pal. *Tarsius.* × 12.

a lateral ventral external. All these areas appear to be present in *Tarsius* and well developed. However, owing to the obliquity of the sections in this region some difficulty has been experienced in comparing these sections with the results obtained by others in the Primate brain. The thalamus can best be appreciated by taking sections through the anterior, middle, and posterior thirds, but this is not possible in my series.

(4) The median nucleus appears to be a differentiation in the thalamus that is regarded as a characteristic of the Primates. This is present in *Tarsius*.

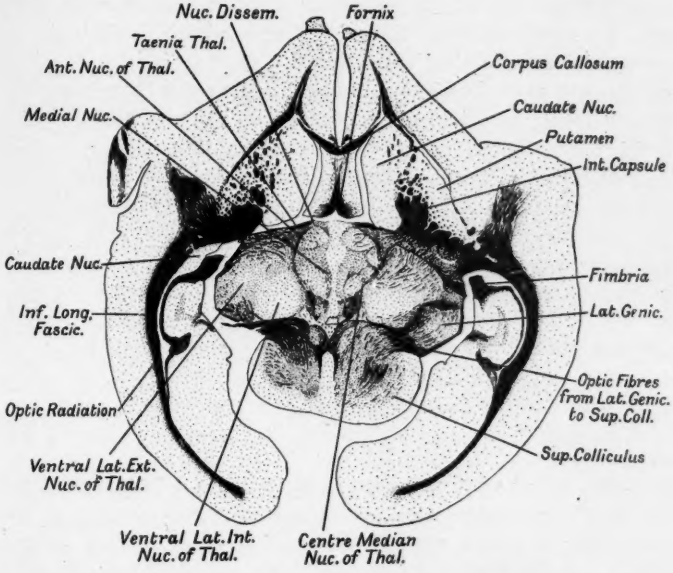


Fig. 5. Nearly horizontal section of brain of *Tarsius*. Weigert-Pal. × 2½.

## EPITHALAMUS

The development of the taenia thalami is greater in the lower animals. Its development is well marked in *Tarsius*. The habenular ganglia lie at the dorso-medial angle of the pulvinar where the striae medullares enter its medial aspect. The medial portion of the ganglion consists of small cells closely packed together. The lateral portion is better developed and consists of large cells. A nucleus intercalatus may be present between the medial and lateral nuclei. Fine fibres enter the medial nucleus, while from the lateral arise much coarser fibres. These fibres together form the fasciculus retroflexus of Meynert.

According to Brunner, *Hapale* approaches the lower mammals in that

both nuclei of the habenular ganglion are well developed and the taenia is particularly large.

In *Tarsius* the conditions would appear to be very similar: for both the medial and the lateral, especially the lateral, appear to be extremely well developed. Moreover the fasciculus retroflexus appears to be quite large.

## THE OPTIC MECHANISMS

The retina, the optic nerve and the lateral geniculate have been described by me elsewhere. The lateral geniculate is interesting since it discloses a well-marked ventral nucleus (dyscritic) concerned with mid-brain reflexes, and a very large and well-laminated dorsal nucleus (epicritic). The investigations of Brouwer have shown that in the Primate series there is a progressive reduction in these mid-brain optic connections. In the higher members of the Primates it is difficult always to demonstrate that optic fibres reach the superior colliculus. However, in *Tarsius* such fibres are extremely abundant. The pulvinar has been excluded (by Brouwer) as a centre which transmits fibres by the optic radiation to the area striata. My sections are very favourable for the determination of such a point; the inference is unavoidable that all the fibres of the optic radiation are derived from the lateral geniculate. The pulvinar is well developed and the fibres which appear to start from it join with the thalamic radiation. Their destination cannot be determined. The formation and distribution of the optic radiation is visible throughout its whole extent and is formed entirely of geniculate fibres.

The characters of the area striata and its extent have been discussed in a previous paper.

The ocular nuclei have been described by Hunter and more recently by Le Gros Clark. The third nucleus is characterised by the presence of a very pronounced Edinger-Westphal nucleus and some suggestion of a nucleus of Perlia.

## THE EIGHTH NERVE

The cochlear division represents the epicritic portion of this nerve and the vestibular the dyscritic element. The anatomy of these two parts of the eighth seems to agree with the descriptions of Winkler and others who have investigated their central connections. The figures that accompany this paper illustrate certain aspects of the nerve. Since nothing can be added to the knowledge of these connections there is no need to describe them in detail. Winkler has recorded how difficult it is in an animal like the rabbit to demonstrate the connection of fibres of the acoustic system with the medial geniculate body. Moreover, since the lateral fillet antedates the development of the cochlea and is therefore present in animals which have no cochlea, it is not possible to regard this as a measure entirely of the development of pure acoustic fibres. In lower animals three areas have been described in

the medial geniculate by Munzer and Weiner. There is a dorsal portion composed of loosely arranged multipolar cells, and a ventral portion of scattered small cells. Surmounting these two there is a cap of large, actively staining cells, the nucleus supra-geniculatus. In both *Tarsius* and *Hapale* the body is homogeneous and in this resembles the medial geniculate of higher animals.

The sections have enabled me to see a large contingent of fibres leaving the antero-mesial aspect of the medial geniculate and joining the internal capsule. The anatomy of the auditory area of the brain has been described elsewhere.

## THE CORPUS STRIATUM

*Tarsius* shows a primitive aspect of cerebral organisation in the fact that the caudate nucleus and putamen are fused over a very large area. The ansa lenticularis and the nucleus of Luys are well developed. The nucleus of Luys shows progressive enlargement in the Primate series. De Vries has recorded the fact that the proportions of the caudate nucleus in its different parts may vary, and he has observed in *Hapale* that the transverse section of the tail in the roof of the inferior horn of the lateral ventricle may be larger than the area of the section of the caudate in the body of the lateral ventricle. Such however is not the case in *Tarsius*. The tail is relatively slender compared with the rest of the caudate nucleus.

The series of sections available for study naturally do not permit any statements on such a controversial point as the relation of the striatum to the cortex.

## RED NUCLEUS

Hatschek was the first to show that the red nucleus comprises two portions, the nucleus magnocellularis from which arises the rubrospinal path, and the nucleus parvocellularis which appears later phylogenetically and reaches its highest development in man and the anthropoids. Monakow has further subdivided the nucleus parvocellularis, but in this he has not been generally followed. Fibre paths of the red nucleus such as the fasciculus rubroreticularis from the lateral portion of the nucleus parvocellularis to the lateral fillet, the rubrothalmic and rubrocortical are also doubtful. The latter, according to Monakow, is best developed in man and passes to the opercular region of the parietal and prefrontal areas.

In *Hapale* (Brunner and Spiegel) there is found just caudal to the nucleus of the third nerve some large cells which represent an excellent development of the nucleus magnocellularis. Cranial to these come irregularly scattered cells indicating the existence of the nucleus parvocellularis. As one follows the red nucleus more cranially it gradually becomes indistinctly separated from the surrounding structures and where the third ventricle begins it disappears. In general these observers regard the nucleus magnocellularis as better developed than the nucleus parvocellularis. This when compared

with what occurs in the Old World monkeys places the red nucleus far below them in development and in fact it closely resembles the form assumed in the rabbit for instance.

An examination of the red nucleus in a variety of lemurs shows that there is very little to distinguish the form of the body in these animals from that present in *Hapale*. *Tarsius*, like the lemurs, has a well-marked nucleus magnocellularis and a diffuse not easily defined nucleus parvocellularis. The same applies to *Nyctipithecus*. It too has a large nucleus magnocellularis. It is therefore concluded that in all these forms the organisation of the red nucleus falls short of what is found in the Old World monkeys. They all show a deficiency in the organisation of the nucleus parvocellularis and exhibit a predominantly large nucleus magnocellularis.

## PONS

Borowiecki has shown that in the pons there can be distinguished six cell groups according to the relationship they bear to the peduncle. Those cells which lie in the vicinity of the peduncle or are interspersed amongst its fibres are described as the peri- or intrapeduncular groups. Those groups which lie around the peduncle are distinguished as lateral, latero-dorsal, medial and ventral. Of these groups the most interesting are the ventral and the intrapeduncular groups, since the former (the ventral) are best developed in lower mammals, whereas the latter only come into existence in the higher groups. Borowiecki has further shown that the lateral, the intra- and peripeduncular groups undergo degeneration whenever the peduncle or the middle brachium of the pons is sectioned. These cell groups are therefore related to the cerebro-pontine-cerebellar system of fibres. The remaining groups give off fibres to the mid-brain, to the formatic reticulars of the pons and probably also to the medulla.

In *Hapale*, as I can confirm, Brunner and Spiegel describe the existence of the paramedial and medial groups. The ventral group is absent caudally but a small ventral group appears near the anterior limit of the pons. The lateral group is well developed, as is also the intrapeduncular group. In regard to the fibres the stratum profundum is poorly developed. In fact there is no group of fibres which could be described as such. Fibrae rectae are very few in number.

*Lemur catta* (Brunner and Spiegel) shows a much better development of the peri- and intrapeduncular fibres than does *Hapale*. The arrangement of the pontine fibres into three groups is also better marked than in *Hapale*.

In *Tarsius*, the general construction of the pons is far more primitive than in either *Lemur* or *Hapale*. In regard to cell formation the ventral group is extremely large and exists throughout the whole extent of the pons. The peduncle which is compact and transversely oval throughout is surrounded by grey matter, but there is only a faint indication of intrapeduncular cells

and no separate groups of peripeduncular cells. The lateral and the medial groups are better marked but not nearly so large as the ventral group. The fibres present an abundant stratum superficiale and a stratum complexum, but no fibres which could be described as a stratum profundum.

Thus *Tarsius* presents the most primitive development of the pons in that the cellular masses connected with the cerebro-pontine fibres are at a minimum whereas those (the ventral nucleus) connected with the formatio reticularis of the brain stem are at a maximum. Moreover the segregation of the fibres into strata is only seen in the superficial fibres. *Hapale* presents an advance on *Tarsius* in that the cerebro-pontine fibres are better marked, while the lemur is still more highly developed.

## OLIVARY NUCLEI

Brunner subdivided the inferior olive into three portions. There is the part which extends farthest spinalwards and lies ventro-laterally. The second part lies more orally and is dorso-medial to the preceding, with which it fuses. The third portion develops from the substantia reticularis lateralis and lies on the lateral side of the first portion. In the lowest mammals these three portions simply lie side by side. In the Primates the second and third portions are rudimentary, but the first part develops considerably. In the case of *Tarsius* the superior olive forms a single convoluted mass of relatively considerable size and is situated in the ventro-lateral area. Its development far exceeds that of the rabbit and is as well advanced as in the cat. Secondly, there is another portion, the inferior olive, which appears on the lateral side of the pyramid soon after the decussation has begun. This part disappears in the oral sections when the better-developed lateral portion, the superior olive, makes its appearance. This medial olive is of simpler construction; it does not become convoluted and is of small extent.

## THE CEREBELLUM

The cerebellum of the Platyrrhines has been described by Bolk. I have described the cerebellum in some detail in order to bring the account of this organ into relation with the systems of Elliot Smith and Ingvar.

The cerebellum exhibits the fundamental subdivisions plainly, and is much like the lemurine cerebellum. There is, however, some increase in the size of the lateral lobes. Bolk has remarked that the simplest form of the cerebellum amongst the Platyrrhines is found in *Hapale*. There is present in this cerebellum complete continuity between the lamellae of the middle portion or vermis and the lateral portions.

The anterior lobe conforms to Bolk's description and contains four lamellae bounded posteriorly by the fissura prima. The fissura prima crosses the superior surfaces of the cerebellum about its middle.

The lobus medius consists of a series of lamellae which are continuous across the middle line. They comprise from before backwards two on the superior surface and two on the posterior surface. Between the lobes springing from the posterior and superior surfaces there are situated between their prolongations laterally three lamellae. These three lamellae superficially do not appear to be connected with the middle portion, though they are fused with the lobus medius deeply.

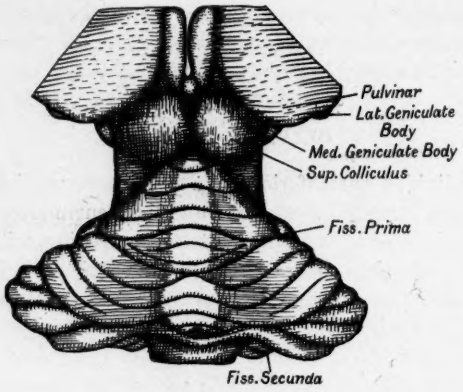


Fig. 6. Dorsal view of brain stem and cerebellum of *Hapale*. × $\frac{7}{3}$.

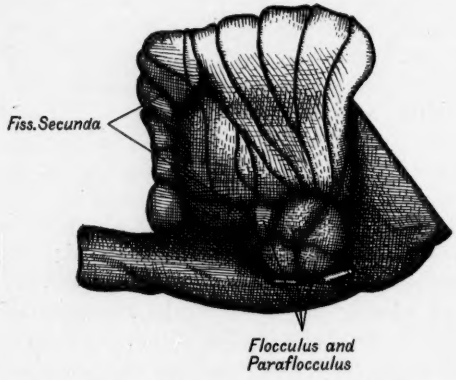


Fig. 7. Lateral view of cerebellum of *Hapale*. × $\frac{7}{3}$.

The posterior face of the cerebellum is practically vertical. Below the portion of the lobus medius on this surface there comes the lobus posticus. The pyramid occupies the middle of this lobe and is superficially fissured. Then comes the uvula. The nodule is completely buried and lies in contact

with the medulla oblongata. The fissure between the lobus posticus and the middle lobe runs laterally below the lateral area of the lateral lobe and becomes the fissura floccularis, separating the paraflocculus and the lateral lobe from each other. In its course behind the lateral lobe it separates two wide lamellae from the middle lobe which carry the lobus posticus to the flocculus and paraflocculus.

These latter two elements are quite large and lie cut off from the lateral lobe above by the fissura prepyramidalis.

The cerebellum is extremely like the cerebellum of *Tarsius*. Bolk has shown that in all lemurs the cerebellum is characterised by the presence of the lobo-paramedianus. This is absent in *Tarsius* and also in the New World

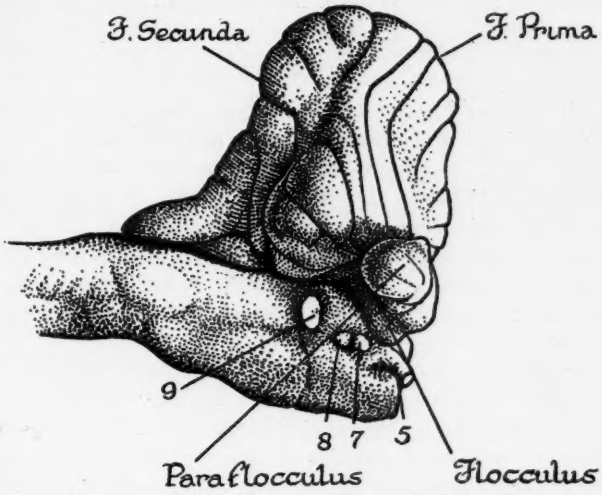


Fig. 8. Lateral view of cerebellum of *Tarsius*. × 6. (From the *Proc. Zool. Soc. London*, 1925.)

monkeys. Therefore, in so far as the cerebellum is concerned, the New World monkeys resemble *Tarsius* more closely than any member of the order Lemuroidea.

Ingvar recalls the interesting observation of Bolk that in the anthropoids, the lamellar system of the lobus anso-paramedianus is not, or is only imperfectly, connected with the vermis. This is the case for instance in the cerebellum of *Anthropopithecus niger*, *Hylobates leucicus* and *Pongo pygmaeus*. In the human cerebellum the inferior semilunar lobule is joined broadly with the tuber valvulae, thus differing from the anthropoids. In *Tarsius* and *Hapale* relations homologous to those in man exist between the middle and the lateral lobes.

Brunner has classified the cerebellar nuclei in accordance with the form they exhibit when they are examined in a series of mammals beginning with

the lowest. In the lowest member there is only a single nucleus divided into two parts by the fastigio-bulbar fibres and fused with the nuclei of the vestibular nerve. As higher members are examined the single nucleus breaks up into fragments, the more medial portions apparently retaining connection with the vestibular nuclei or in the highest members indirectly by means of fibre connections. The lateral part becomes distinct as the nucleus dentatus and has no relation with the vestibular nuclei but gives origin to the fibres of the superior peduncle. In *Hapale* and *Tarsius* the condition of the cerebellar nuclei seems to have reached an identical state of differentiation. The lateral or dentate nucleus is large and is obviously the source of the peduncular fibres. A single median nucleus is present, the nucleus interpositus, and in more oral sections this fuses with the lateral nucleus.

## SUMMARY

The brain stem of *Tarsius* exhibits, as do so many other features of its anatomy, a combination of characters which at once make it very primitive and very advanced. Its zoological importance will vary according as to whether one emphasises one aspect of its anatomy and neglects the other. If both are kept in mind, one must agree with Elliot Smith that it constitutes one of those forms that so very nearly represent a basal stock. Whatever factors then have brought about evolution, it is difficult to escape the conclusion that all the existing Primates have started from a Tarsioid stock, of which the existing Tarsier is the representative.

The efferent side of its neural organisation is easily the least developed. Elsewhere I have noted the slight characterisation of the motor area and the slender pyramidal columns. The primitive states of the basal ganglia, the red nucleus, the pons and cerebro-pontine systems have been noted in the present paper. On the other hand, the sensory side shows distinct signs of progress. This is evident in the fifth nerve, in the optic mechanisms, and in the organisation of the thalamus. Donaldson long ago showed the superior development of the sensory side of the nervous system and the great enhancement this undergoes in the cephalic region. Hence one would anticipate that, given the zoological position of *Tarsius*, indications should appear in sensory mechanisms of the emergence of a higher level of epicritic appreciation. To show that vision should be the predominant epicritic mechanism in Primate evolution has been the work of Elliot Smith.

(1) An attempt has been made to consider the brain stem of *Tarsius* in terms of a generalised conception of epicritic and dyscritic neural mechanisms.

(2) Indications of epicritic advance have been shown in the optic, the eighth and the trigeminal systems and also in the posterior columns in *Tarsius*.

(3) On the efferent side the neural mechanisms remain exceedingly primitive.

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# THE RELATIONS OF THE HYALOID CANAL IN THE FOETUS AND IN THE ADULT[1]

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**Running forwards through the vitreous body from the entrance of the optic nerve to the posterior surface of the lens, is the hyaloid canal, filled with lymph and lined by a prolongation of the hyaloid membrane.**

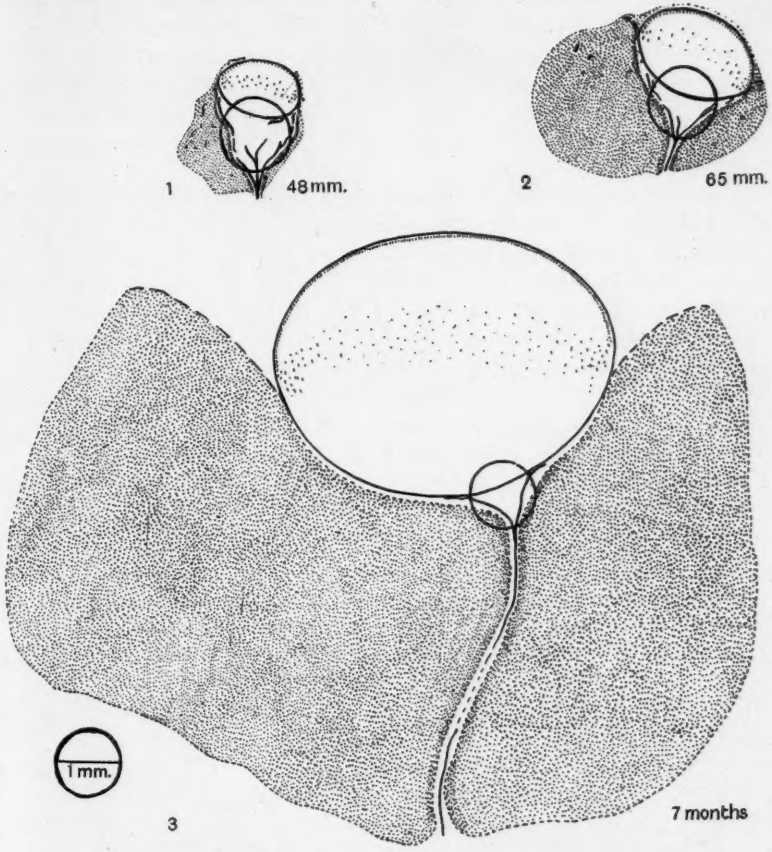
**Gray's *Anatomy*, 23rd ed., 1926, p. 1024.**

A STATEMENT to this effect (with an accompanying diagram) finds a place in all works on the anatomy of the eye, despite the fact that its verification is difficult and that few attempts are ever made to demonstrate its truth. The existence of the Canal of Cloquet in man has never been seriously questioned, although it cannot normally be seen either in microscopic sections of the adult eye or in the living subject with the ophthalmoscope. The older anatomists demonstrated it occasionally by means of dyes allowed to flow along it, but the main argument for its existence in the adult is the ease with which it can be seen in the foetus. On its development and its early appearance has been built up the standard description of its final condition and relations. The difficulty of demonstrating it in the adult eye is due to two factors. Firstly, the vitreous is partially destroyed and so altered in appearance by fixation that reliable microscopic sections of it are very hard to obtain. Secondly, the freshly excised eye is difficult to dissect, and the hyaloid membrane is so injured by even the gentlest of manipulations, that gross observation usually fails to reveal anything conclusive. It was, however, pointed out in a previous paper in this *Journal* that a new and promising method of examination of the anterior parts of the eye was now available, namely bio-microscopy with the Gullstrand slit-lamp. With this instrument it is possible to examine the surface of the hyaloid membrane lining the fossa patellaris during life. When this was first done it was noticed that no funnel-shaped opening passing back into the vitreous could be seen, and the possibility of the canal of Cloquet normally disappearing completely after birth had to be considered. That this is not the case, however, can be shown by further investigation by the same method, and the present paper is an attempt to demonstrate by correlation of bio-microscopical and embryological findings what may be considered the normal relations of the canal from foetal to adult life.

The first embryonic stage which concerns us is that of 48 mm. This is the time, in human embryos, at which the foetal intra-ocular blood system is at

[1] Under a grant from The Medical Research Council.

its maximum. Every subsequent stage reveals a retrogression of some portion of it. Fig. 1[1] shows the vitreous body and lens of such a stage (48 mm.). The posterior surface of the lens and the terminal branches of the hyaloid artery are enclosed by a circle, the diameter of which represents 1 mm. It is




Figs. 1, 2 and 3. Three stages in the development of the vitreous and Cloquet's canal, seen at the same magnification. The lens is shown in outline in the upper part of each figure. The secondary vitreous is dotted.

apparent that the artery divides before it reaches the lens and that its branches spread out and form a sort of vascular cone or funnel applied to the lens. The diameter of the mouth of this funnel is at this stage only a little less than that of the lens itself and is roughly 1 mm. The vitreous filling the funnel and

[1] The figures, which are drawn to scale, are diagrammatic and give no indication of the appearance of the tissue, which is actually fibrillar, not granular.

surrounding the hyaloid artery is more open in texture than that outside it, and will be referred to as the primary vitreous[1]. The rest of the vitreous body is referred to as the secondary vitreous. It is closer in texture and stains more deeply than the primary vitreous. The primary vitreous containing the vessels does not lie, even at this stage, in the centre of the eye but rather towards the nasal side. Horizontal sections of left eyes are shown in the first three drawings and in each it is apparent that the amount of secondary vitreous is larger on the temporal side of the hyaloid canal than on the nasal. It is to be noticed in fig. 1 that the secondary vitreous only comes into direct contact with the lens at the equator, the rest of the posterior lens surface abutting on primary vitreous.

From the 48 mm. stage onwards the increase in size of the vitreous body is brought about by increase of the secondary vitreous only. At 65 mm. (fig. 2) the branches of the hyaloid artery still arise from the main trunk (which has itself increased in length) a little less than a millimetre behind the lens, and form a vascular cone of a similar size to that seen in the previous stage, although the size of the vitreous as a whole has increased considerably. This is apparent on comparing the portions within the small circles in figs. 1 and 2, the magnification of which is the same. The displacement of the canal towards the nasal side of the eye is even more marked than in the previous stage. There is a condensation, which was foreshadowed at 48 mm., on the surface of the secondary vitreous, separating it from the primary vitreous. This condensation is the so-called hyaloid membrane, and is continuous with the wall of Cloquet's canal. It is to be noted that the hyaloid membrane is adherent to the lens capsule just behind the equator only. The wall of Cloquet's canal is separated from the lens capsule by the primary vitreous which fills the fossa patellaris.

After the 65 mm. stage the most marked change in the appearance of the vitreous is due to the atrophy of the intra-ocular vascular system. The secondary vitreous increases enormously in size and is quite avascular. The main trunk of the hyaloid artery increases in length but becomes thinner. The cone of branches on the back of the lens remains of the same size (roughly 1 mm. in diameter at its base) as in previous stages but the branches are fewer and become, by the seventh month, extremely atrophied. The original area of the posterior capsule in contact with the base of the vascular cone can still be recognised as a small circular region (situated slightly below and to the nasal side of the exact posterior pole of the lens) which sometimes presents a slightly stippled appearance and sometimes appears to be enclosed by a narrow line. The area is formed by the cone of vessels, not by the mouth of Cloquet's canal, which is simply continuous with the hyaloid membrane and is not adherent to the lens capsule. The hyaloid membrane itself is adherent to the lens capsule, slightly behind the equator only, as it was in previous

[1] Druault's nomenclature for the regions of the developing vitreous is made use of for convenience. The question of the accuracy of his theories regarding it is not under discussion.

stages. Fig. 3 shows diagrammatically the relations of the vessels, the wall of Cloquet's canal, and the hyaloid membrane, to the lens capsule of a seven months human foetus. The magnification and the size of the small circle enclosing the bifurcating artery are the same as in figs. 1 and 2. The similarity

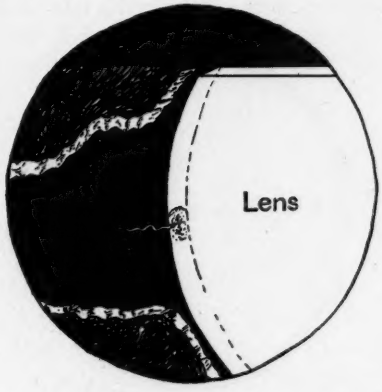



Fig. 4. Slit-lamp appearance of Cloquet's canal in infancy.

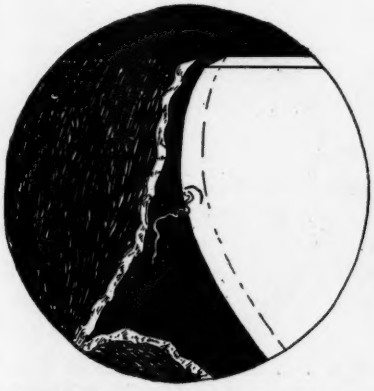


Fig. 5. Slit-lamp appearance of Cloquet's canal in a child.

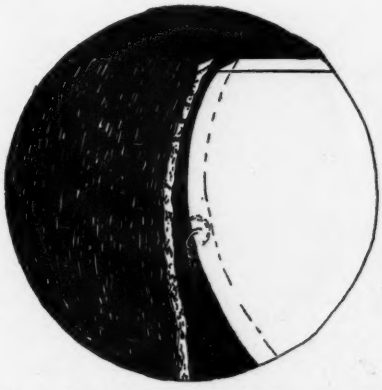


Fig. 6. Slit-lamp appearance of the retro-lental space and the hyaloid remnant in a normal adult.

of the region enclosed by the circle in all three diagrams is obvious. It will be seen that, apart from the existence of actual vessels at this stage, the condition is similar to that figured for the adult in most text-books.

The subsequent changes which occur are the result of continued atrophy of the vessels. During the eighth month the main trunk of the hyaloid artery

becomes impervious to blood in its central portion, and here gradually atrophies and disappears. It is well known that atrophying vessels in the vitreous (e.g. the vasa hyaloidea propria (Versari)) as they lose connection with their trunk of supply, tend to curl up and assume corkscrew forms. This is no doubt due to the presence of a certain amount of elastic tissue in their walls. The main trunk of the hyaloid is no exception to this rule. It begins to curl during

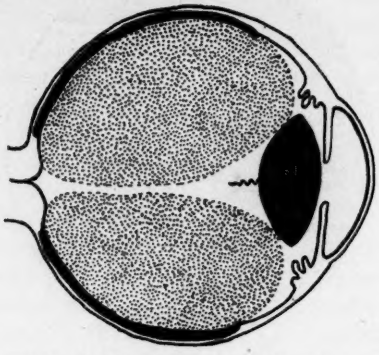


Fig. 7. *A*. The relations of Cloquet's canal at birth.

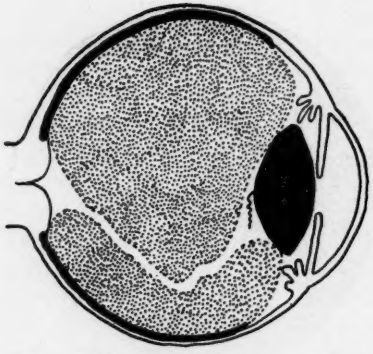


Fig. 7. *B*. The relations of Cloquet's canal in the adult with the eye at rest.

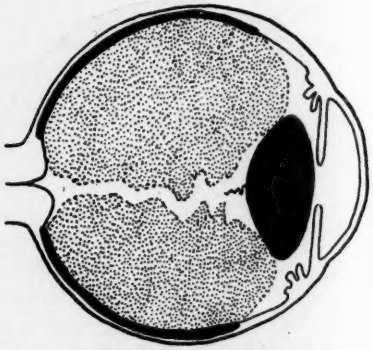


Fig. 7. *C*. Momentary relations of Cloquet's canal in the adult eye after sudden movement upwards.

the latter part of foetal life, and at birth looks like a fine wavy white thread extending straight backwards from just below and to the nasal side of the posterior pole of the lens. The walls of Cloquet's canal, now at some distance from the atrophic vascular remnant, extend horizontally backwards towards the disc. These appearances can be seen with the slit-lamp both in fresh eyes of stillborn foetuses and, more easily, in the living eyes of children of variable

ages up to four years and often older. Fig. 4 shows the slit-lamp aspect[1]. The faint curved line enclosing a faintly stippled area within which the hyaloid artery breaks up is known to clinical workers as the "arc line" (Bogenlinie (Vogt)). It can be measured in the living eye at all ages and always has a diameter of roughly 1 mm. Thus no actual growth can occur in the terminal branches of the hyaloid artery after the 48 mm. stage.

Usually at or before the age of four the horizontal hyaloid remnant of infancy begins to sag under the influence of gravity and with it the walls of Cloquet's canal, which become extremely lax. Fig. 5 shows the appearance in the eye of a child of twelve in whom the process of sagging was not yet complete, the hyaloid remnant making an angle of about 45° with the posterior surface of the lens. The coincident sagging of the wall of Cloquet's canal can be seen. The upper wall now passes downwards and backwards practically parallel with the direction of the hyaloid remnant. The lower wall can just be seen. It has almost dropped below the lower border of the pupil. The hyaloid remnant has become more curly.

This process of sagging continues and is usually complete before puberty. Fig. 6 shows the normal condition in the adult as seen with the slit-lamp. The hyaloid remnant hangs down like a corkscrew behind the lens. The walls of Cloquet's canal have sagged so much that the opening cannot be seen through the pupil. The hyaloid membrane (front face of the (secondary) vitreous) can, however, be seen to slope downwards and backwards behind the lens, and would, if it could be followed, lead to the open mouth of the canal. This can be made to float up into view if the subject be asked to look downwards and then quickly upwards again. If the coincident movement of the vitreous be watched with the slit-lamp the canal will be seen to float up and to assume for a second or so its foetal position. As it settles down again it passes through the various developmental positions described, and its appearance at successive seconds as it falls is similar to that seen in figs, 4, 5 and 6. The space between the lens and the hyaloid membrane seen in fig. 6 is known to slit-lamp workers as the "retro-lental space." It is obviously the fossa patellaris or hyaloid fossa of anatomists and from an embryological point of view contains primary vitreous continuous with that surrounding the vessels in Cloquet's canal.

These appearances can be seen, by anyone conversant with the use of the slit-lamp, in the great majority of normal adult eyes. Individual differences in the length of the hyaloid remnant, the shape of the arc line and the density of the hyaloid membrane are extremely common, but the presence of the backward slope of the vitreous face and some indication of the position of

[1] In studying slit-lamp diagrams it is to be remembered that the appearance obtained with the instrument is that of a fairly thick section, seen stereoscopically, of the transparent parts of the eye. The lens appears greyish, the primary vitreous almost black, the secondary vitreous very dark grey and fibrillar, and the vascular remnants and the hyaloid membranes as white threads and wrinkled diaphanous sheets. It is impossible to represent the exact appearances in a black and white drawing.

the hyaloid remnant are practically invariable, even in advanced life. One can therefore conclude that the minimal persistence of the central end of the hyaloid artery and the displacement of Cloquet's canal into the lower part of the eye are normal. Fig. 7 shows diagrammatically the relations of Cloquet's canal at birth and in the adult.

In conclusion we may consider that the presence of Cloquet's canal as an anatomical structure throughout life is vindicated by the most certain of methods, namely, intra-vitam microscopy. The usual median horizontal position assigned to it in text-books is inaccurate if the body be supposed to be in the anatomical attitude. Further its situation may vary on movement or under the influence of gravity. Another anatomical fact, namely, that minimal persistence of the lental end of the hyaloid artery is normal in man, has been brought to light by the same method.

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# A NOTE ON THE DEVELOPMENT OF THE ASCENDING COLON

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The development of the ascending colon has not been given the attention that its importance would appear to warrant. In most text-books there is but the slightest reference to it. In them, and in the many papers dealing with the abnormalities of this part of the gut and of the caecum and appendix, there constantly occurs the phrase "descent of the caecum," and there is almost a consensus of opinion that the ascending colon is formed as the caecum descends from a position high up in the abdominal cavity under the liver; that is, that there is an elongation of an originally short part through the downward growth of the caecum.

The whole description of the development of the ascending colon, given in the last edition of Quain's *Anatomy* (1), is as follows: "The U-shaped loop of the large intestine is produced by its proximal portion being carried to the right, so that it comes to be transversely disposed, passing from right to left. As it lengthens the caecum descends to assume its definitive position in the right iliac fossa, and thus we have laid down an ascending and a transverse colon." Hertwig's description (2) is as follows: "Dann tritt erst von der Flexura coli dextra aus ein rückläufiges Langenwachstum ein, wodurch das Colon ascendens entsteht und das Caecum in die rechte Fossa iliaca gelangt."

These descriptions do not take into account the important changes which occur in the size of the liver, relative to the size of the abdominal cavity, from the early stages of development; and that the liver during these early stages of development extends downwards almost as far as the upper limit of the iliac cartilages.

A dissection of a human foetus soon after the intestinal loop has been withdrawn from the umbilical coelom into the abdominal cavity shows the relative positions of the costal margin, liver, caecal anlage, and iliac crest (fig. 1); and it clearly demonstrates that the caecum is not placed high up in the abdominal cavity, but that with the liver it is placed well down and close to the highest point of the iliac crest.

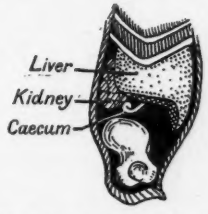


Fig. 1. Dissection from the side of a human foetus of 6 cm. C.R. length, showing the relative positions of liver, caecal anlage, and iliac crest.

When the umbilical loop of intestine is withdrawn from the umbilical

coelom into the abdominal cavity, the colon passes obliquely from the level of the right iliac crest, below the lower pole of the right kidney, upwards and to the left to an ill-marked, rounded splenic flexure, skirting on its way the greater curvature of the stomach, already at this stage of development of a definite shape (fig. 2). In this oblique part of its course the colon crosses the second part of the duodenum and folds the latter against the dorsal abdominal wall, and where this occurs an adhesion is formed between the colon and the duodenum (3). This adhesion is an important landmark in the study of the development of the ascending colon, for the changes which take place in its formation occur around this point.

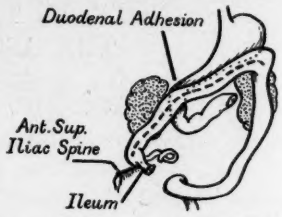


Fig. 2. The first stage in the development of the ascending colon, as it appears in a dissection of a human foetus of 13·5 cm. C.R. length.

With the further growth of the colon the gut shows two definite bulgings which quickly become well-marked curves; the segment of the gut between the duodenal adhesion and the caecal anlage forms a gentle curve convex to the right, and the segment between the adhesion and the splenic flexure a curve with the convexity directed caudally. By the further increase in length of the colon, these two curves become more distinct (fig. 2); the segment on the right of the duodenal adhesion assumes an oblique direction and makes a sharp angle at the point of adhesion with the left segment of the gut, while the latter becomes still more curved and no longer in strict apposition with the greater curvature of the stomach. At this stage, the right and left segments are connected to the dorsal abdominal wall by a common mesentery, but the right segment, by its continued growth, now makes a rotation on its own long axis from left to right, turning over on the anterior surface of the right kidney (fig. 3). The mesentery of this part of the gut is thus brought against the parietal peritoneum of the dorsal abdominal wall, and the two adjacent layers being now practically immovably fixed against one another, fuse; the mesentery of this part of the colon disappears and the bowel is left firmly fixed in the normal retroperitoneal position of adult anatomy.

According to these observations the segment of the colon lying between the caecal anlage and the duodenal adhesion forms the whole of the ascending colon and that part of the transverse colon which lies between the hepatic flexure and the adhesion. Further, a comparison of the relation of the caecal anlage and the lower pole of the right kidney in the early stages of the development of the colon, shows that the segment of the gut does not descend as is usually described, but that there is an actual ascent of the upper end of the ascending colon, a change brought about by the increase in length of the right segment of the gut and associated with the rotation of this part of the colon.

The irregular growth of the caecum which produces the bulging of its anterior wall tends to give the appearance of a downward movement, but this is apparent rather than real and is merely a "flowing over" of the irregularly developed sac, the caecum, held in position at the relatively fixed ileo-colic junction.

Just after the return of the gut from the umbilical coelom to the abdominal cavity the ileo-colic junction is found at, or just above, the level of the highest point of the iliac crest. In the series of foetuses of the 3rd month examined in this investigation the ileo-colic junction was never placed higher than 3 mm. above this point, and at this stage there was no pouching of the gut to indicate the caecum. In the complete series of human foetuses examined, from the 3rd to the end of the 9th month, the ileo-colic junction was rarely

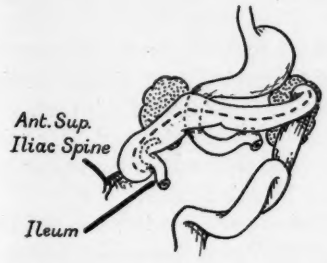


Fig. 3. The second stage in the development of the ascending colon, as it appears in a dissection of a human foetus of 20 cm. C.R. length.

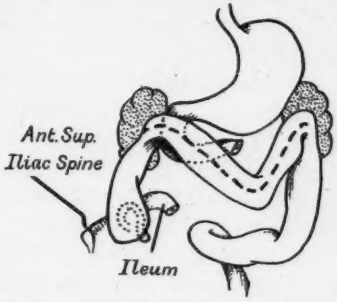


Fig. 4. The third stage in the development of the ascending colon, as it appears in a dissection of the human foetus of 23 cm. C.R. length.

more than 3 mm. above the iliac crest and never more than 5 mm. above this point. Up to the beginning of the 6th month the gut at the position of the caecum, although gently dilated, showed no trace of anything in the nature of pouching or sacculation.

In a series of 20 adult bodies examined in the dissecting room of Belfast University, the ileo-colic junction was found at, or just above, the level of the inter-tubercular plane in 12 cases; just below the level of this line in 4 cases; and just below the level of the brim of the true pelvis in 4 cases. That is, in 80 per cent. of cases the ileo-colic junction had retained its primitive position, and in only 20 per cent. of cases had it sunk down into the pelvis. The inter-tubercular plane is the level given in almost all text-books of anatomy for the "surface marking" of this portion of the gut. In those cases in which the ileo-colic junction had assumed a pelvic position, a generalised visceroptosis was present; in these 4 cases, therefore, it is taken as being in an abnormal position.

The direction of the longitudinal taeniae of the adult ascending colon suggests that a rotation has occurred, for the ventral band of longitudinal

muscle fibres in the transverse colon curves round at the hepatic flexure and appears on the right dorso-lateral surface of the ascending colon, while the ventral longitudinal band of fibres of the ascending colon bends below the hepatic flexure to reach the infra-dorsal surface of the transverse colon. If further proof of the rotation of the ascending colon were needed, a study of those subjects in which an ascending meso-colon is present supplies it. In these cases the ventral longitudinal band of fibres of the ascending colon does not pass below the hepatic flexure to reach the infra-dorsal surface of the transverse colon but is continued as the ventral band of this part of the colon.

## SUMMARY

(1) The developing colon, when withdrawn from the umbilical coelom, does not pass transversely from right to left on the abdominal wall, but passes obliquely from the right iliac crest upwards and to the left to the splenic flexure.

(2) An adhesion occurs between the second part of the duodenum and the part of the colon where the two cross, and the subsequent changes in the formation of an ascending and a transverse colon occur around this part.

(3) The segment of colon between the duodenal adhesion and the caecal anlage forms the whole of the ascending colon and that part of the transverse colon between the duodenal adhesion and the hepatic flexure.

(4) A rotation occurs on the ascending colon from left to right and the ascending meso-colon becomes fixed against the dorsal abdominal wall and disappears.

(5) If this rotation does not occur an ascending meso-colon is found in the adult.

(6) During these changes, the ileo-colic junction remains as a relatively fixed point within a few millimetres of the margin of the iliac crest.

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# SOME OBSERVATIONS ON THE CERVICAL SYMPATHETIC IN MAN

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Within recent years the anatomy of the cervical sympathetic has attracted attention on account of the operations described by Jonnesco (5) and others, e.g. Daniélopolu (2), Holmes and Ranson (3), for angina pectoris, Graves' disease, and certain other conditions, but more especially on account of the operation of sympathetic ramisection devised by Royle (9, 10, 11), in collaboration with the late Prof. Hunter (4), for the treatment of spastic paralysis. Realising the need of more accurate anatomical information as a guide to the surgeon in performing the operation of ramisection, Potts (8) has recently published a description, accompanied by a series of excellent plates, of the main peripheral connections of the human sympathetic.

The subject-matter of the present communication is based on nine complete dissections of the cervical sympathetic, as well as on the examination of parts of it in about a dozen other specimens. In connection with this investigation a cast has been made, under my direction, of a complete dissection of the whole sympathetic chain and its rami communicantes, and has been placed in the Anatomical Museum of the University of Otago. Although in the main my findings agree with those of Potts, certain points appear to me worthy of further discussion, and I also desire to add a more detailed description of the course of the rami communicantes in the specimens which I have dissected.

The observations which are recorded in the following pages fall under three main headings: (A) The arrangement of the cervical ganglia, (B) The histological structure of the cervical ganglia, and (C) The arrangement of the rami communicantes in the cervical region.

## A. THE ARRANGEMENT OF THE CERVICAL GANGLIA

Text-book descriptions, e.g. Cunningham (1), Piersol (6), Poirier and Charpy (7), and Spalteholz (12), usually mention three ganglia, viz. superior, middle, and inferior, as being normally present. It is, however, not infrequently added that the middle ganglion may be absent. Both Cunningham and Poirier and Charpy further state that the middle ganglion may be divided into two parts, a fact which they regard as evidence of its morphological derivation from the Vth and VIth cervical ganglia.

Both Potts (8) and Jonnesco (5) agree that the middle cervical ganglion may be absent. In addition, Potts describes two common positions in which the

middle ganglion, when present, may be found; while Jonnesco states that in some cases the middle ganglion is represented by a number of small thickenings on the sympathetic chain. Further, Jonnesco describes a fourth cervical ganglion, also inconstant, which he terms the intermediate ganglion; according to his description, this ganglion, when present, lies ventro-medial to the vertebral artery at the root of the neck and is cephalic to the inferior cervical ganglion; he states that it is as frequently present as is the middle ganglion, and that it may occur either in the presence or in the absence of a middle ganglion.

It is, then, evident that the superior and inferior cervical ganglia are definite large thickenings of the sympathetic chain, situated respectively high up and low down in the neck; that both are invariably present; and that there is little or no variation in their position. With regard to these ganglia I have nothing to add to what has already been recorded: variations in their shape and size are well known, as is also fusion or non-fusion of the inferior cervical ganglion with the Ist thoracic ganglion, to which I shall refer in connection with the rami communicantes to the Ist thoracic nerve.

On the other hand, the position with regard to the middle cervical ganglion is far from clear, and more evidence is required as to the significance of the intermediate ganglion of Jonnesco. Although I have investigated only a comparatively small number of cases, the following points will, I think, be of interest.

### 1. *Regarding the Middle Cervical Ganglion*

In the great majority of cases which I have examined the middle cervical ganglion was present as a definite thickening of the sympathetic chain. Such cases, as has also been noted by Potts, fall into two types: (*a*) those in which the middle cervical ganglion lies in close association with the inferior thyroid artery at about the level of the VIth cervical vertebra; and (*b*) those in which the middle cervical ganglion lies on the ventral aspect of the vertebral artery at about the level of the VIIth cervical vertebra; the former may be termed the high type, and the latter the low type, of middle cervical ganglion. In the cases which I have examined the low type occurred more frequently than the high. The condition on opposite sides of the neck is not necessarily the same.

(*a*) *In the high type* (fig. 1), the ganglion takes the form of a flattened, oval or ovoid thickening resting on the longus colli muscle at the level of the Vth or VIth cervical transverse process, being most often in relation to the carotid tubercle of Chassaignac. It has an important relation with the inferior thyroid artery where this vessel bends medially to pass dorsal to the carotid sheath, for which reason, according to Poirier and Charpy (7), it has been termed by Haller the "thyroid ganglion." It may lie a little above or a little below the bend in the artery, though I found it most often lying directly behind the vessel. Jonnesco (5) describes it as being often split by the artery, which then passes through it as through a button-hole; in such cases he states that the main bulk of nerve fibres passes up through the posterior limb of

the loop. The high type of ganglion gives rami communicantes constantly to the Vth and VIth cervical nerves, occasionally also to the IVth or even to the IIIrd cervical nerve.

(*b*) *In the low type* (fig. 2), no thickening is present on the sympathetic chain at the level of the VIth cervical vertebra, but a pyramidal enlargement of the chain lies directly on the ventral or ventro-medial aspect of the vertebral artery 1 to 3 cm. above its origin, this level being generally that of the VIIth

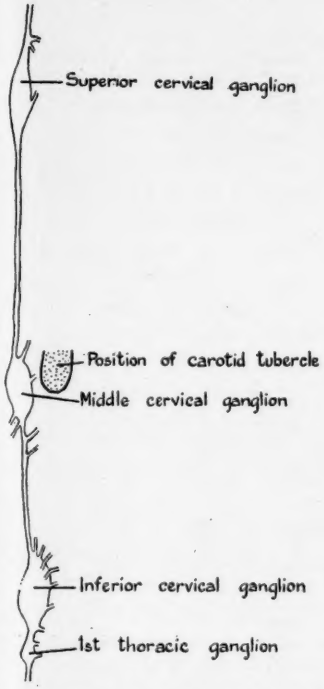


Fig. 1. Left cervical sympathetic chain with middle ganglion in its high position.

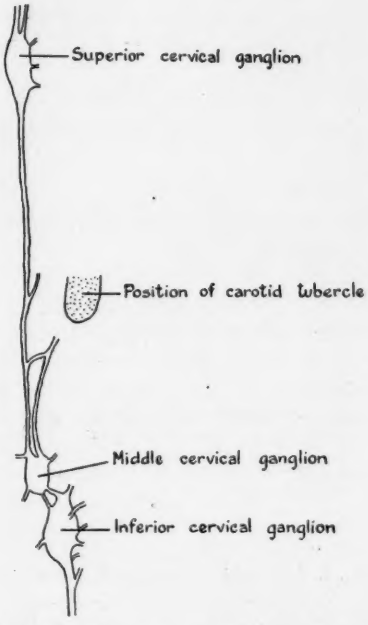


Fig. 2. Left cervical sympathetic chain with middle ganglion in its low position.

cervical vertebra. This ganglion is connected to the inferior cervical ganglion in two ways: firstly, by the ansa subclavia encircling the first part of the subclavian artery, and, secondly, by two bands which encircle the vertebral artery to join the inferior cervical ganglion, which lies dorsal to that vessel. The rami communicantes from the low type of ganglion are distributed most frequently to the Vth and VIth cervical nerves, but there is some variation in that I have seen rami proceeding from it to the Vth cervical nerve alone, and to the Vth, VIth, and VIIth cervical nerves.

Three cases among those which I have examined did not conform to either of these two types.

In two of these cases it appeared at first sight that no middle cervical ganglion was present. After careful dissection, however, it was clear that a small thickening of the chain existed on the ventral aspect of the vertebral artery in the exact position occupied by the low type of middle cervical

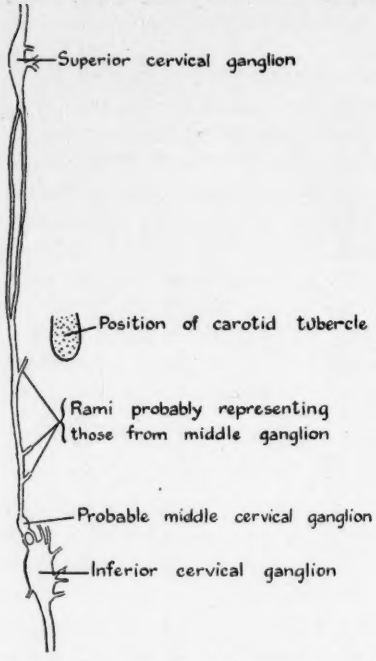
Superior cervical ganglion
Position of carotid tubercle
Rami probably representing those from middle ganglion
Probable middle cervical ganglion
Inferior cervical ganglion

Fig. 3. Left cervical sympathetic chain with apparent absence of the middle cervical ganglion. This figure shows a small thickening in the position of a low type of middle ganglion, but no rami communicantes arise from it. See text for possible explanation.

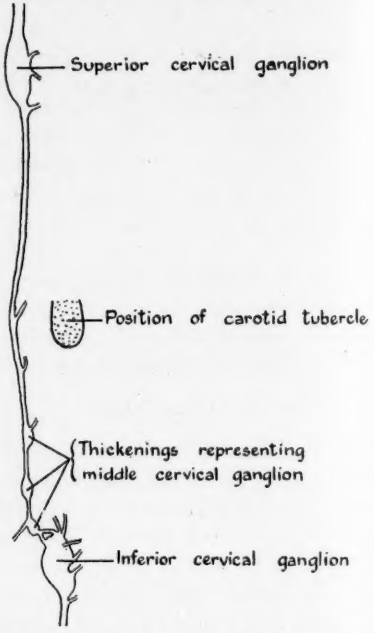


Fig. 4. Left cervical sympathetic chain with apparent absence of the middle cervical ganglion. Three thickenings of the chain, each showing actual nerve cells microscopically, evidently represent a "multiple ganglia" condition of the middle ganglion.

ganglion (fig. 3), but it gave no rami communicantes to the cervical nerves. The following points make it at least possible that this small thickening was actually a middle cervical ganglion: firstly, that it occupied the same position as a definite middle cervical ganglion of the low type; secondly, that the rami communicantes to the Vth and VIth cervical nerves, though not proceeding from this small thickening, arose from the trunk immediately above it (fig. 3), as though they had "slipped up" a little (this condition is often present in

cases of a definite middle ganglion either of the high or of the low type, and affects one or more rami communicantes); and, thirdly, that on histological examination the small thickening was found to contain nerve cells.

In the third of the atypical cases (fig. 4), the middle cervical ganglion was represented by a small thickening lying on the ventral aspect of the vertebral artery and by two smaller thickenings on the chain above this—the condition of multiple ganglia mentioned by Jonnesco. On histological examination the three small thickenings were found to contain nerve cells.

### 2. *Regarding the Intermediate Cervical Ganglion of Jonnesco*

In its position and in its relation to the vertebral artery the intermediate ganglion of Jonnesco obviously corresponds to the low type of middle cervical ganglion (fig. 2) described in this paper.

Jonnesco, however, as has already been pointed out, states that his intermediate ganglion may occur either in the presence or in the absence of a middle cervical ganglion.

In those cases where, according to Jonnesco, his intermediate ganglion exists in the absence of a middle cervical ganglion, I contend, from my observations on the rami communicantes, that we have before us simply a low type of middle cervical ganglion. In those cases where, according to Jonnesco, both his intermediate ganglion and the middle cervical ganglion are present at the same time, I would suggest that either, firstly, the middle ganglion is present in its high position and a small piece of it is cut off and lies in the low position, or, secondly, that the middle ganglion is represented by two thickenings, one in the position of the low type of middle cervical ganglion (this being Jonnesco's intermediate ganglion) and the other on the chain just above this—the first stage in the production of the condition of multiple ganglia representing the middle cervical ganglion.

## B. THE HISTOLOGICAL STRUCTURE OF THE CERVICAL GANGLIA

In the following statements Jonnesco (5) throws doubt on the true ganglionic nature of certain of the thickenings of the cervical sympathetic chain which from their macroscopic appearance would be described as ganglia:

(1) "En effet, au niveau de l'artère thyroidienne inférieure, où se trouve ce ganglion (i.e. the middle cervical ganglion), quand il existe, le cordon sympathétique peut présenter un renflement, pareil à d'autres qui peuvent exister sur tout le trajet du cordon, sans être le véritable ganglion cervical moyen."

(2) "Au-dessous du ganglion intermédiaire, qui, ainsi que le ganglion moyen, n'a que l'apparence d'un ganglion nerveux, mais histologiquement n'est qu'un simple renflement nerveux, nous trouvons la masse ganglionnaire formée par l'union du dernier ganglion cervical au premier thoracique."

With the object of verifying the above statements, I examined a number of ganglia taken from dissecting-room subjects and from post-mortems, and in all cases I found nerve cells present.

## C. THE ARRANGEMENT OF THE RAMI COMMUNICANTES IN THE CERVICAL REGION

As it is with these fine nerves that the surgeon is concerned in the operation of Sympathetic Ramisection, I have carefully investigated their course in a number of cases, giving special attention to those which proceed to the roots of the brachial plexus. In the main my dissections confirm the account given by Potts(8), but I have noticed a few new facts, and in this section of the paper I propose to give a detailed account of the course taken by the rami in the cases which I have examined.

In the first place it is important to distinguish between true rami communicantes and other extremely numerous branches of the sympathetic, e.g. visceral and arterial. In general it is possible to differentiate between the two sets of branches by the direction which they take in their course from the sympathetic chain. Thus, the visceral branches to the pharynx, larynx, thyroid gland, heart, etc. are directed (*a*) in the upper part of the neck, medially and a little forwards, and (*b*) in the lower part of the neck, downwards, medially, and forwards. On the other hand, the rami communicantes are directed (*a*) in the upper part of the neck, directly outwards, and (*b*) in the lower part of the neck, either directly upwards, or upwards and backwards, or upwards and outwards. In my figures, all of which are drawn from actual dissections, I have, with one or two exceptions, purposely omitted, for the sake of clearness, all branches of the sympathetic other than true rami communicantes. The direction of the rami communicantes shown in the figures will be seen to agree with the general statement of their direction given above.

The individual rami communicantes will be described according to the spinal nerves to which they proceed.

### 1. *Grey Rami to the first four Cervical Nerves, i.e. to the Nerves of the Cervical Plexus*

The first four cervical nerves are commonly united by communicating links forming three large loops just at, or a little lateral to, the lateral border of the rectus capitis anticus major muscle.

The grey rami to these nerves (figs. 5, 6 and 12) generally arise from the superior cervical ganglion on its lateral or anterior aspect, and they are usually three in number, as follows:

(*a*) The uppermost is a short filament joining either the Ist cervical nerve, just as it appears lateral to the rectus capitis anticus minor muscle, or the loop between it and the IInd cervical nerve.

(*b*) The middle ramus is a similar short branch joining either the IInd cervical nerve or the loop between it and the IIIrd cervical nerve.

(*c*) The lowest ramus arises from the lower part of the ganglion and joins either the IIIrd cervical nerve or the loop between it and the IVth cervical nerve.

In many cases these are the only grey rami to the first four cervical nerves. I have, however, observed the following variations in this arrangement.

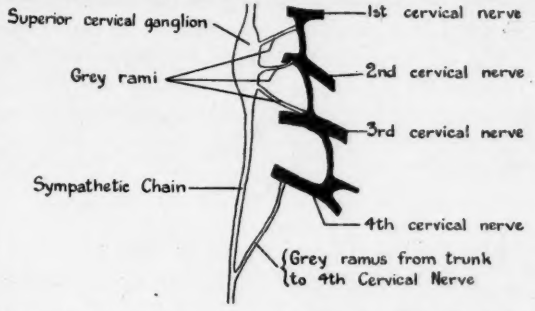


Fig. 5. A typical arrangement of rami communicantes to the first four cervical nerves. Left side of neck.

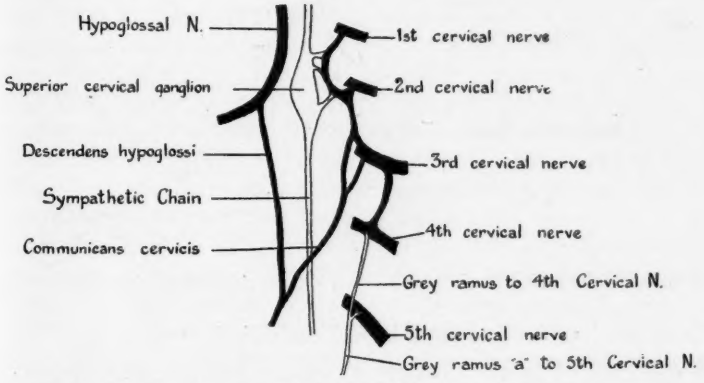


Fig. 6. Showing a ramus to the IVth cervical nerve arising from a ramus to the Vth cervical nerve. Left side of neck.

(1) The uppermost ramus may be double.

(2) The lowest ramus may be absent.

(3) Another grey ramus may be present, passing to join the IVth cervical nerve. This ramus is interesting in that it does not arise from the superior cervical ganglion. It is commonly present in the absence of the lowest of the three rami which arise from that ganglion. Frequently it takes origin from the sympathetic trunk at about the level of the carotid tubercle (figs. 5 and 12);

it then passes upwards and slightly outwards across the surface of the rectus capitis anticus major, and joins the IVth cervical nerve on its anterior aspect just after it has emerged from the lateral border of that muscle. In other cases (fig. 6) it is a continuation upwards of a ramus to the Vth cervical nerve, which joins the latter just above and lateral to the carotid tubercle; it is a fine filament passing upwards anterior to the Vth cervical nerve, and is just overlapped by the lateral border of the rectus capitis anticus major; occasionally it is continued still further cranially to join the IIIrd cervical nerve in a similar manner.

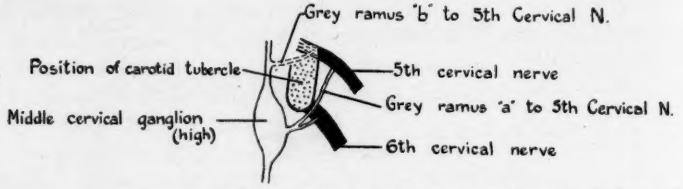
Grey ramus 'b' to 5th Cervical N.
Position of carotid tubercle
5th cervical nerve
Grey ramus 'a' to 5th Cervical N.
Middle cervical ganglion (high)
6th cervical nerve

Fig. 7. Showing two rami to the Vth cervical nerve, the constant ramus "a" from a high middle ganglion, and the first inconstant ramus "b." Left side of neck.

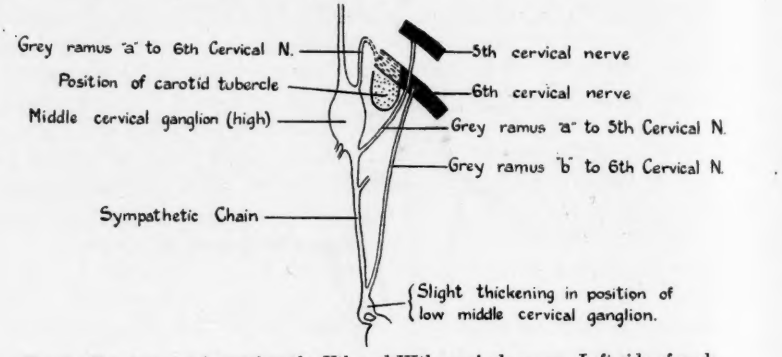
Grey ramus 'a' to 6th Cervical N.
5th cervical nerve
Position of carotid tubercle
6th cervical nerve
Middle cervical ganglion (high)
Grey ramus 'a' to 5th Cervical N.
Grey ramus 'b' to 6th Cervical N.
Sympathetic Chain
Slight thickening in position of low middle cervical ganglion.

Fig. 8. Showing certain rami to the Vth and VIth cervical nerves. Left side of neck.

### 2. *Grey Rami to the Vth Cervical Nerve*

In the cases which I have examined the Vth cervical nerve receives either one or two or three grey rami. Of these, one was present in all cases and will therefore be termed here the constant grey ramus; the other two, which were not present in all cases, may be termed inconstant.

(*a*) *The constant grey ramus.* See figs. 7 to 10, where it is labelled "Grey ramus 'a' to 5th Cervical N."[1]; it is also indicated in figs. 6 to 12.

[1] In figs. 5 to 13 the grey rami to the Vth, VIth, VIIth and VIIIth cervical nerves are labelled with reference to the sections of the text in which they are described. Thus, "Grey ramus 'a' to 5th Cervical N." is the ramus described in the text under heading (*a*) of the rami to the Vth cervical nerve; "Grey ramus 'c' to 6th Cervical N." is the ramus described under heading (*c*) of the rami to the VIth cervical nerve; and so on.

It is a fine filament which arises either directly from the middle cervical ganglion (whether this be of the high or of the low type) or from the sympathetic trunk just above a low type of middle ganglion.

When it arises from a middle cervical ganglion of the low type (fig. 9), it passes upwards and outwards across the vertebral artery and thus reaches the superficial surface of the scalenus anticus muscle close to its origin. Here it is often joined by a small branch which leaves the trunk at the level of the carotid tubercle. It passes upwards across the scalenus anticus, winds closely round the lateral aspect of the carotid tubercle, and joins the Vth cervical nerve (where it lies in the groove on the upper surface of the Vth cervical transverse process) on its anterior or antero-inferior aspect; the point of junction is just at the lateral border of the rectus capitis anticus major.

When this ramus arises either from the sympathetic trunk above a middle ganglion of the low type or directly from a middle ganglion of the high type (figs. 7 and 8), it passes more directly across the vertebral artery to reach the superficial surface of the scalenus anticus; thereafter its course is the same as above.

This ramus exhibits the following variations in its course and termination: (1) it may pierce some fibres of the scalenus anticus before reaching the lateral aspect of the carotid tubercle; (2) it may divide, before reaching the Vth cervical nerve, into two branches, one of which then joins the VIth cervical nerve (fig. 7); (3) it may be prolonged upwards as a fine filament passing to join the IVth cervical nerve (fig. 6); this has already been described in connection with the grey rami to the first four cervical nerves.

(*b*) *The first inconstant ramus* (fig. 7). This was present in the great majority of my specimens. It arises from the sympathetic trunk just above the carotid tubercle. Either immediately or after an upward course of a few millimetres, it pierces the longus colli muscle, running posteriorly through the muscle close to the disc between the IVth and Vth cervical vertebrae. It passes either medial or lateral to the vertebral artery, and joins the Vth cervical nerve as it lies in the groove of the Vth cervical transverse process. It has in addition some connections with the vertebral arterial plexus.

(*c*) *The second inconstant ramus* (fig. 11). This is a fine branch arising from a ramus which accompanies the vertebral artery and which is mainly distributed to the VIth cervical nerve. (See ramus described under heading (*c*) of the grey rami to the VIth cervical nerve.)

### 3. *Grey Rami to the VIth Cervical Nerve*

I have dissected four distinct grey rami communicantes to this nerve. One of these ((*c*) below), which arises from the inferior cervical ganglion, was present in every case. Of two others ((*a*) and (*b*) below), which arise from the middle ganglion or from the sympathetic trunk, one or other was always present, and in quite a number of cases both were present. A fourth ramus ((*d*) below), arising from the inferior ganglion, was present in two cases, in

both of which only one ramus from the middle ganglion was present. It would thus appear that in any given case the VIth cervical nerve may receive either two or three grey rami communicantes, each of which has a definite course and should be carefully searched for at operation.

(*a*) *A ramus arising either from a middle cervical ganglion of the high type, or from the trunk immediately above it, or from the trunk just above a middle ganglion of the low type* (figs. 8 and 12). This is a short ramus running upwards for a few millimetres from its origin and then piercing the longus colli muscle just above the level of the carotid tubercle and just below a similar branch to the Vth cervical nerve which has already been described. It passes posteriorly through the muscle close to the disc between the Vth and VIth cervical vertebrae to join the VIth cervical nerve as it lies in the groove of the VIth cervical transverse process. In all cases it passed medial to the vertebral artery in order to join the nerve.

In all cases in which the middle cervical ganglion was of the high type, this ramus was present and arose from that ganglion or from the trunk immediately above it. When, however, the ganglion is of the low type, the ramus is inconstant but may still be present as a branch from the trunk at the level of the VIth cervical vertebra, irrespective of the presence or absence of another ramus from the ganglion itself to the same cervical nerve (*vide infra*).

(*b*) *A ramus arising either from a middle cervical ganglion of the low type or from the trunk just above this level* (figs. 8, 9, 10 and 12). This is a long fine branch which passes upwards anterior to the lower cervical nerve roots. It crosses the anterior aspect of the vertebral artery obliquely as the artery is proceeding upwards to the foramen in the VIth cervical transverse process. It then reaches the superficial surface of the scalenus anticus muscle, across which it runs, lateral to the carotid tubercle, to join the VIth cervical nerve just under cover of the rectus capitis anticus major.

In the case of this ramus I have observed the following variations: (1) it may receive a connection from the trunk just above the middle cervical ganglion; (2) it is often continued (fig. 6) upwards at the lateral border of the rectus capitis anticus major in order to join the Vth cervical nerve, as described above in connection with ramus "a" to the Vth cervical nerve (variation 2); (3) it often pierces the upper part of the scalenus anticus just below the carotid tubercle and just before joining the nerve.

When the middle cervical ganglion was of the low type, this ramus was present in most cases and arose from that ganglion. When the ganglion is of the high type, the ramus may be present as a branch from the trunk just above the slight thickening which in my cases was invariably present on the ventral aspect of the vertebral artery.

(*c*) *A constant ramus arising from the inferior cervical ganglion* (figs. 10 and 11). In my series of specimens this ramus was constantly present, and is quite distinct from the ramus which has just been described.

It is a fairly thick branch arising from the deeper part of the inferior

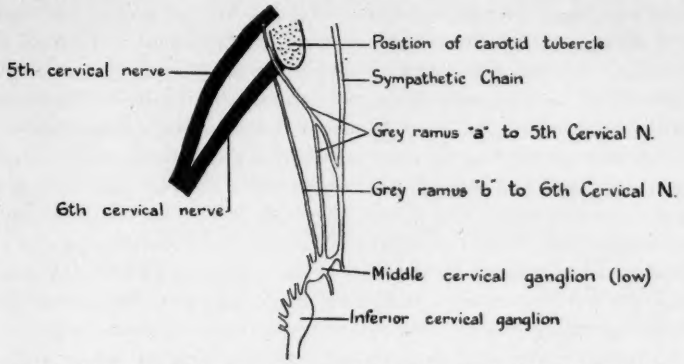
5th cervical nerve
6th cervical nerve
Position of carotid tubercle
Sympathetic Chain
Grey ramus "a" to 5th Cervical N.
Grey ramus "b" to 6th Cervical N.
Middle cervical ganglion (low)
Inferior cervical ganglion

Fig. 9. Showing rami from a middle cervical ganglion in the low position to the Vth and VIth cervical nerves. Right side of neck.

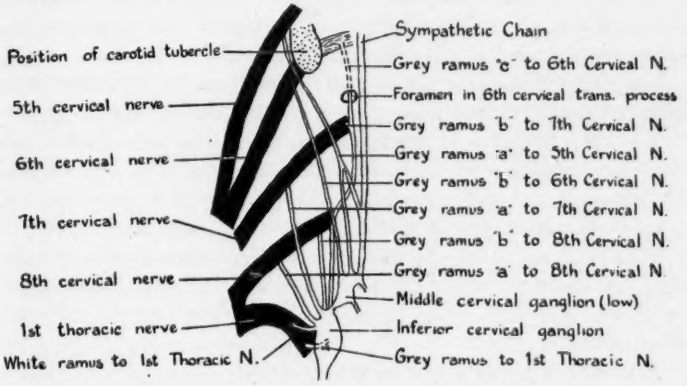
Position of carotid tubercle
5th cervical nerve
6th cervical nerve
7th cervical nerve
8th cervical nerve
1st thoracic nerve
White ramus to 1st Thoracic N.
Sympathetic Chain
Grey ramus "c" to 6th Cervical N.
Foramen in 6th cervical trans. process
Grey ramus "b" to 7th Cervical N.
Grey ramus "a" to 5th Cervical N.
Grey ramus "b" to 6th Cervical N.
Grey ramus "a" to 7th Cervical N.
Grey ramus "b" to 8th Cervical N.
Grey ramus "a" to 8th Cervical N.
Middle cervical ganglion (low)
Inferior cervical ganglion
Grey ramus to 1st Thoracic N.

Fig. 10. Showing some of the rami arising from a middle cervical ganglion in the low position and from the inferior cervical ganglion. Right side of neck.

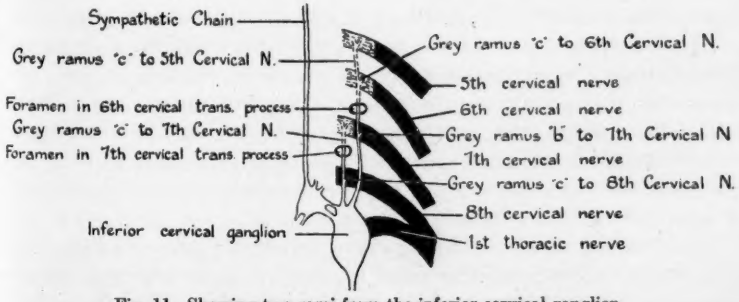
Sympathetic Chain
Grey ramus "c" to 5th Cervical N.
Foramen in 6th cervical trans. process
Grey ramus "c" to 7th Cervical N.
Foramen in 7th cervical trans. process
Inferior cervical ganglion
Grey ramus "c" to 6th Cervical N.
5th cervical nerve
6th cervical nerve
Grey ramus "b" to 7th Cervical N
7th cervical nerve
Grey ramus "c" to 8th Cervical N.
8th cervical nerve
1st thoracic nerve

Fig. 11. Showing two rami from the inferior cervical ganglion (all others omitted). Left side of neck.

cervical ganglion. It runs upwards along the medial side of the vertebral artery, anterior to the vertebral vein, and to the lateral side of the longus colli muscle; it is thus situated in a narrow isosceles triangle, as mentioned by Potts, and bounded as follows: (*a*) medially, by the lateral border of the longus colli muscle; (*b*) laterally, by the vertebral artery; and (*c*) inferiorly—the short base of the triangle—by the neck of the first rib, with the inferior cervical ganglion lying in front of it. In its course upwards from the ganglion the ramus crosses anteriorly, in turn, the neck of the first rib (if the ganglion is below this), the VIIIth cervical nerve, and the transverse process of the VIIth cervical vertebra. At this point it gives some of its fibres to the VIIth cervical nerve; these fibres join the nerve just lateral to its emergence from the intervertebral foramen. The ramus then courses upwards anterior to the VIIth cervical nerve, and, in company with the vertebral artery, enters the foramen in the transverse process of the VIth cervical vertebra.

By removing the anterior bar of the VIth cervical transverse process and then displacing laterally the vertebral artery and its venae comites, I have found that the ramus either wholly or in part joins the VIth cervical nerve either in or just lateral to the intervertebral foramen. In a few cases careful dissection revealed the fact that some of the fibres of the ramus continued upwards in front of the VIth cervical nerve and passed through the arterial foramen in the Vth cervical vertebra to join the Vth cervical nerve in a similar manner. (See ramus referred to under heading (*c*) of the rami to the Vth cervical nerve.)

It has been clear to me, in the course of my dissections, that many of the fibres from this ramus become incorporated in the sympathetic plexus surrounding the vertebral artery. But I have been surprised at the comparative ease with which definite connections with the cervical nerves mentioned can be demonstrated.

The ramus has been noticed by others but its significance has not, to my knowledge, previously been stressed. Jonnesco (5) describes the branch in this position as an arterial branch *receiving* fibres from the Vth, VIth, and VIIth cervical nerves, showing that he had noted the connections which it has with these nerves. Spalteholz (12), on the other hand, mentions that branches of the vertebral arterial plexus are rami communicantes. The latter view seems to me to be very reasonable; and, while I am convinced from my own observations that the branch described above is a grey ramus to the VIIth and VIth cervical nerves, and frequently also to the Vth, I believe further that it is not at all unlikely that many fibres leave the vertebral arterial plexus throughout its course in the neck and are distributed to the seven cervical nerves with which it comes into intimate relation.

(*d*) *An inconstant ramus arising from the inferior cervical ganglion.* The ramus which has just been described was, as has already been pointed out, present in all my cases, and I have seen no variation in its course. In two cases, however, a second ramus to the VIth cervical nerve arose from the

inferior cervical ganglion. This was a fine branch accompanying the vertebral artery upwards for some distance, and crossing that vessel on its anterior aspect from within outwards. At the point where the artery entered the arterial foramen in the VIth cervical transverse process, the ramus left the artery to pass more laterally, pierced the scalenus anticus muscle, and joined the VIth cervical nerve just below the carotid tubercle. Its point of junction with the nerve was under cover of the upper fibres of the scalenus anticus.

### 4. *Grey Rami to the VIIth Cervical Nerve*

Commonly three grey rami communicantes are connected with the VIIth cervical nerve. Of these three, two were constant in my specimens and one inconstant; in certain cases one of the constant rami is represented by two or three separate filaments; thus, in any given case, the number of rami present may vary from two to five. All take origin from the inferior cervical ganglion.

(*a*) *The first constant ramus* (fig. 10). This is a well-defined nerve leaving the upper part of the inferior cervical ganglion and running upwards and laterally to join the VIIth cervical nerve on its inferior aspect either just medial to the lateral border of the scalenus anticus muscle or under cover of the muscle. It is from 1·5 to 2·5 cm. long, and during its course crosses the VIIIth cervical nerve anteriorly. The relation of the ramus to the scalenus anticus muscle is very variable. When the VIIth cervical nerve lies directly between the scalenus medius and scalenus anticus muscles, the ramus, before reaching the nerve, may cross partly the anterior surface of the scalenus anticus, pierce the muscle, or run entirely deep to it. When the VIIth cervical nerve is found piercing the muscle or even lying in front of it, the ramus correspondingly either pierces the muscle or lies in front of it.

The ramus is often accompanied by a similar branch running parallel to it on its medial side, and joining the VIIth cervical nerve immediately above it. In one case (fig. 12), I found three parallel rami in this position running upwards and outwards to join the VIIth cervical nerve under cover of the scalenus anticus muscle.

(*b*) *The second constant ramus* (figs. 10 and 11). This ramus is fully discussed above under heading (*c*) of the rami to the VIth cervical nerve.

It courses upwards on the medial aspect of the vertebral artery at the lateral border of the longus colli muscle. It passes anterior to the VIIIth cervical nerve and the transverse process of the VIIth cervical vertebra, and then joins the VIIth cervical nerve either in or just lateral to the intervertebral foramen. It then continues upwards through the arterial foramen to the VIth, and sometimes also to the Vth, cervical nerves.

(*c*) *A third ramus frequently present in addition* (figs. 11 and 12). This ramus I found in the great majority of cases. It was sometimes a very definite strong ramus, and at other times extremely thin and delicate. It springs from the postero-superior aspect of the inferior cervical ganglion, and runs upwards

and a little backwards in close association with the vertebral vein. After crossing anterior to the VIIIth cervical nerve, to which it may give a small filament, it enters the foramen in the transverse process of the VIIth cervical vertebra in company with the vertebral vein. It joins the VIIth cervical nerve in the intervertebral foramen between the VIth and VIIth cervical vertebrae.

### 5. *Grey Rami to the VIIIth Cervical Nerve*

The grey rami to the VIIIth cervical nerve vary in number from two to five. Two alone are constant, but one of these may be represented by two, three, or four separate filaments. They are shorter than any of the preceding rami communicantes, the longest being only 2 cm. in length, and the average 1 cm. They all arise from the inferior cervical ganglion.

(*a*) *The first constant ramus* (figs. 10, 12 and 13). A well-defined thick branch, 1 to 2 cm. in length, arises from the lateral or superior aspect of the inferior cervical ganglion and courses upwards and outwards, often crossing the head or neck of the first rib, and joining the VIIIth cervical nerve as it lies behind the scalenus anticus muscle. It joins the nerve on its inferior, or less commonly on its anterior, aspect. It lies posterior to the first part of the subclavian artery, and bears a varying relation to the superior intercostal artery, being either superficial or deep to it, and in either case very intimately related to it.

The ramus is generally double and may be in three distinct branches. In one case I dissected four fine but distinct rami communicantes running parallel courses upwards and outwards to join the VIIIth cervical nerve deep to the scalenus anticus muscle or at its medial border.

(*b*) *The second constant ramus* (figs. 10 and 12). This is a short thick ramus arising from the upper pole of the inferior cervical ganglion, and running vertically upwards medial and posterior to the vertebral artery, a few millimetres lateral to the lateral border of the longus colli muscle. It passes in front of the transverse process of the first thoracic vertebra, medial to the first costo-central articulation, and joins the VIIIth cervical nerve on its anterior aspect just as it emerges from the intervertebral foramen.

(*c*) *A third ramus frequently present in addition* (fig. 11). This is a branch of the ramus described under heading (*c*) of the rami to the VIIth cervical nerve. This ramus runs upwards in company with the vertebral vein, and is medial to the ramus just described ((*b*) above), as seen in fig. 12. In most cases (fig. 11) this ramus gives a filament to the anterior aspect of the VIIIth cervical nerve as it crosses the latter on its way to the foramen in the VIIth cervical transverse process, but in some cases I could find no such connection with the VIIIth cervical nerve.

### 6. *Rami Communicantes to the Ist Thoracic Nerve*

An important feature of the Ist thoracic nerve is the fact that, in addition to having grey rami communicantes similar to those of the cervical nerves, it has also a white ramus communicans—the first of a series of 13 or 14 white

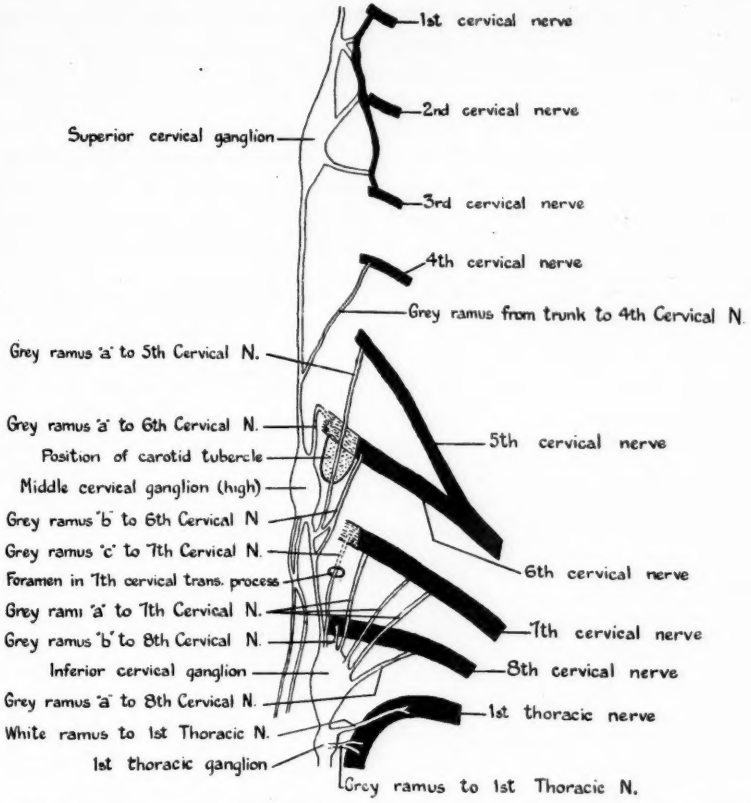
1st cervical nerve
2nd cervical nerve
Superior cervical ganglion
3rd cervical nerve
4th cervical nerve
Grey ramus from trunk to 4th Cervical N.
Grey ramus 'a' to 5th Cervical N.
Grey ramus 'a' to 6th Cervical N.
5th cervical nerve
Position of carotid tubercle
Middle cervical ganglion (high)
Grey ramus 'b' to 6th Cervical N
Grey ramus 'c' to 7th Cervical N.
6th cervical nerve
Foramen in 7th cervical trans. process
Grey rami 'a' to 7th Cervical N.
7th cervical nerve
Grey ramus 'b' to 8th Cervical N.
Inferior cervical ganglion
8th cervical nerve
Grey ramus 'a' to 8th Cervical N.
1st thoracic nerve
White ramus to 1st Thoracic N.
1st thoracic ganglion
Grey ramus to 1st Thoracic N.

Fig. 12. Showing the arrangement of a number of rami communicantes in a dissection where the middle ganglion was in its high position. Left side of neck. The Ist thoracic ganglion is separated from the inferior cervical ganglion. The Ist thoracic ganglion has been retracted medially to put the rami on the stretch, and therefore the grey ramus to the Ist thoracic nerve is shown running laterally; actually this ramus runs almost directly backwards.

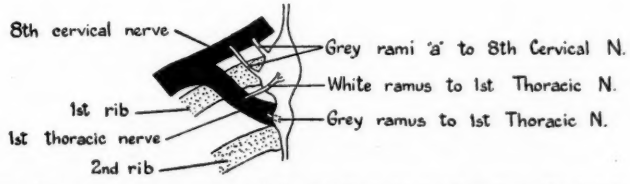
8th cervical nerve
Grey rami 'a' to 8th Cervical N.
White ramus to 1st Thoracic N.
1st rib
Grey ramus to 1st Thoracic N.
1st thoracic nerve
2nd rib

Fig. 13. Showing apparent separation of the Ist thoracic ganglion from the inferior cervical ganglion. The Ist white ramus however arises from the inferior cervical ganglion, while the grey ramus to the Ist thoracic nerve arises from the Ist thoracic ganglion.

rami communicantes which are present in connection with all the thoracic and the Ist, or sometimes the first two or even the first three, lumbar nerves. The importance of this white ramus communicans lies in the fact that in the operation of cervical ramisection it must not be divided, but is left in order to preserve especially the dilator fibres to the radial musculature of the iris.

(*a*) *The grey ramus communicans to the Ist thoracic nerve* (figs. 10, 12 and 13). Though generally single, this ramus is not infrequently double, the total thickness of the two being then about equal to that of the ramus when single. Even when single it often divides and joins the Ist thoracic nerve in two filaments.

It arises either from the inferior cervical ganglion or from the Ist thoracic ganglion if this is distinct from the inferior cervical ganglion.

In the majority of cases only one grey ramus is present, and takes the form of a short thick band arising from the posterior aspect of the lower half of the inferior cervical ganglion. It runs a course of only a few millimetres practically straight backwards (sometimes a little upwards) to join the anterior aspect of the Ist thoracic nerve where it lies in front of the neck of the first rib; it joins the nerve only a few millimetres lateral to its point of emergence from the intervertebral foramen. The ramus is completely covered anteriorly by the inferior cervical ganglion, which must be turned aside in order to expose it.

The ramus is almost always medial to the superior intercostal artery. Indeed, I regarded this as a constant relation until in one case I found it definitely superficial to the artery and joining the Ist thoracic nerve lateral to it.

This ramus, or the two branches representing it, seems to me to be most difficult of surgical approach. A consideration of the deep situation of the inferior cervical ganglion will serve to show the difficulty of reaching, identifying, and severing the ramus at operation.

(*b*) *The white ramus communicans to the Ist thoracic nerve* (figs. 10, 12 and 13). In every case which I have dissected the first white ramus communicans has been a well-defined and easily differentiated single nerve.

For convenience its course will be described from the inferior cervical ganglion to the Ist thoracic nerve, without regard to the direction of the impulses which it carries.

The white ramus communicans arises as a rule from the inferior cervical ganglion, sometimes from the Ist thoracic ganglion as will be discussed below. It may arise either from the upper or from the lower part of the inferior cervical ganglion, most often from the lateral aspect of the lower part, and always at some distance (1 to 5 mm.) below the origin of the grey rami communicantes to the cervical nerves. It courses almost directly outwards for about 1 cm., and joins the Ist thoracic nerve on its anterior aspect where the nerve is crossing anterior to the neck of the first rib; its direction, though principally outwards, is also slightly backwards, and, according as it arises

from the upper or from the lower part of the ganglion, respectively slightly downwards or slightly upwards. It joins the nerve at a point some distance lateral to the point of junction of the corresponding grey ramus. It is relatively longer than the grey ramus, and it lies anterior to the superior intercostal artery.

The chief points of distinction between the white and the grey rami are summarised in Table I.

Table I.

| White Ramus | Grey Ramus |
|---|---|
| 1. Paler in colour—almost white | 1. Darker in colour—greyish |
| 2. Leaves the ganglion from its lateral aspect and generally from its lower part | 2. Leaves the ganglion from its posterior aspect and always from its lower part. |
| 3. If the above distinction is not clear, the white ramus leaves the ganglion lateral to the grey ramus | 3. If the above distinction is not clear, the grey ramus leaves the ganglion medial to the white ramus |
| 4. Runs in a lateral direction | 4. Runs in a posterior direction |
| 5. Joins the Ist thoracic nerve lateral to the grey ramus | 5. Joins the Ist thoracic nerve medial to the white ramus |
| 6. Nearly always runs anterior to the superior intercostal artery, and joins the nerve lateral to the point where the artery crosses the nerve | 6. Nearly always runs posterior or medial to the superior intercostal artery, and joins the nerve medial to the point where the artery crosses the nerve |
| 7. Longer than the grey ramus | 7. Shorter than the white ramus |

I have noticed the following variations in the origin of the rami communicantes to the Ist thoracic nerve.

Frequently the inferior cervical ganglion is divided by a constriction into a larger upper and a smaller lower mass. In these cases it is usual for both the grey and the white rami communicantes to the Ist thoracic nerve to arise from the lower portion of the ganglion (fig. 12), which no doubt represents the Ist thoracic ganglion only partly incorporated in the inferior cervical ganglion. In two cases, however, in which this division of the inferior cervical ganglion existed, although the grey ramus to the Ist thoracic nerve arose from the lower part, the first white ramus arose unmistakably from the upper part of the ganglion (fig. 13).

Occasionally a completely separate Ist thoracic ganglion exists, connected with the inferior cervical ganglion by a thick trunk about 1 cm. in length. In such cases both the white and the grey rami communicantes to the Ist thoracic nerve arise from the Ist thoracic ganglion.

## SUMMARY AND CONCLUSIONS

1. The observations contained in this paper are based upon nine complete dissections of the cervical sympathetic, as well as on the examination of parts of it in about a dozen other specimens.

2. The superior and inferior cervical ganglia are present in fairly constant positions in all cases, but great variability is found in the condition and position of the middle cervical ganglion.

3. As regards the middle cervical ganglion, the great majority of cases fall into two types, which are here termed the high and low types respectively. In the low type, which occurred more commonly, the ganglion lies in close association with the vertebral artery at the level of the VIIth cervical vertebra. In the high type, which occurred less commonly, the ganglion lies in close association with the inferior thyroid artery at the level of the VIth cervical vertebra.

4. In a few cases the middle cervical ganglion appeared at first sight to be absent, but in these cases a small thickening existed in the position occupied by a middle cervical ganglion of the low type. Reasons are given for regarding this thickening as representing the middle cervical ganglion.

5. Jonnesco has thrown doubt on the true ganglionic nature of some of the thickenings which macroscopically appear as ganglia on the cervical sympathetic. A number of such thickenings have been examined histologically, and nerve cells were found to be present in all cases.

6. The rami communicantes are described in detail, the description of the rami to any given nerve being based on all the specimens examined. Attention is drawn to certain grey rami communicantes which accompany the vertebral artery through the foramina in the cervical transverse processes, and which have not previously been stressed.

7. A number of points of distinction between the grey and white rami communicantes to the Ist thoracic nerve are indicated in Table I.

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# THE ACTION OF THE M. MENTALIS IN THE EXPRESSION OF THE EMOTION OF DISTRESS

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In the *Journal of Anatomy*, October 1925, appeared an article describing the facial muscles which surround the rima oris, and a series of photographs therein showed the action of these muscles during speech and the emotion of laughter. This latter was the only emotion which could be depicted by the subject with verisimilitude, which is easy to understand as it alone of the emotions can be evoked readily in persons not trained to the mummers' art; yet the contrasted emotion of distress is equally distinctive and arouses curiosity as to its exact causation. The classical descriptions of this emotion seem inadequate or even misleading, as no account is taken of the very important part played by the M. mentalis, a powerful and misunderstood muscle which already has been shown (*op. cit.*) in activity during speech and will presently be shown active during the emotion of distress. The observations which form the basis of the following description were obtained from many sources, viz.:

1. The crying of infants and young children. There has been ample material for observation in both these groups. Their emotions were simple ones and they had no qualms about expressing them freely, also their troubles were from such minor causes that one did not feel to intrude upon their privacy nor yet to embarrass them as would certainly have been the case with an adult person.

2. The suppressed tears of older children were likewise observed freely.

3. The distress of adult people when under the influence of alcohol. These "maudlin drunk" folk unfortunately were not often met with as they could be regarded with all the equanimity of children, and apparently were very similar in their manner of expressing emotion.

4. The distress of adult people. The observations made under this group have not been many nor easy to make. The causes of distress in adults which was great enough to break through the barrier of reserve as a rule have been so poignant that anatomical curiosity was almost smothered.

5. The melancholia of the insane. Thanks to the courtesy of Dr Gavin Morton, the Superintendent of one of the largest hospitals for the treatment of the insane in this city, a large number of the melancholy insane were seen. Many of these confirmed the observations made under the headings 1, 2, 3, 4 and 6, but in so many of these people the look of utter hopelessness to a large extent obscured the distress that might still have been present.

6. Various photographs, drawings, paintings or reproductions of paintings and reproductions of statuary, especially that of the Laocoon group. This last might seem to have been discussed fully hitherto, but it confirmed so faithfully all the other sources of information that it were a pity to omit it. The depiction of distress in paintings did not seem to be common and in the Sydney Art Gallery only three examples were to be found, and in one of these, "The Widower," by Luke Fildes, the only figures expressing distress have their mouths and chins covered.

Some bound volumes of *Punch* (London) were also consulted and confirmatory evidence obtained in many of the cartoons or larger drawings. In the smaller drawings, liberties had purposely been taken to accentuate the expression the artist wished to depict.

With regard to the figures accompanying this article, a short explanation of their construction seems necessary. A tracing of the illustration of a norma facialis of a skull, No. 57 in Spalteholz, vol. I, formed the basis on which was drawn an appropriate outline, and alterations were made for the opening of the jaw in other figures. The teeth have been retained throughout as guides, though in some of the expressions, e.g. in infants, they are solecisms. Conventional slits with radiating "crow's feet" have been used for the eyes and are the same in each figure—a conventional outline has been adopted for the nose and there is no shading or thickening of any of the lines. This has been done so as not to distract the attention from, nor to accentuate in any manner the expression of the mouth and nasolabial folds. Conventional markings have been used to denote the alteration in shape of the swelling of the chin caused by the activity of the M. mentalis. In each figure two small crosses indicate the positions of the angles of the mouth when the face is in repose.

When an appropriate mouth had been drawn into each mask the nasolabial folds were inserted close to the angle of the mouth when the oral slit was wide and at some distance from it when the oral slit was narrow. In this respect it must be remembered that the lateral width of the open mouth is inversely proportional to its vertical depth, and that when an attempt is made to increase both simultaneously the rima oris is circular almost. Of necessity the activities of all the circumoral muscles which take part in the expression of grief cannot be determined accurately until chance reveals some person with histrionic ability who is afflicted with a lipodystrophy; the activities of many can be inferred from previous observations of these muscles (*op. cit.*) and the pitting of the skin of the chin and an increased swelling of the chin will always denote activity of the M. mentalis.

Virchow (*Archiv f. Anat. u. Physiol., Anat. Abt.* 1908) has shown that the fibres of the M. mentalis form a series of loops or arches with varying degrees of obliquity which enclose between them a large fibrous and at times a small fatty pad, also that the fibrous pad rests upon a bursa which intervenes between it and the subjacent symphysis menti. These loops or arches are formed

either by the interlacement or the direct continuity of the fibres of the two component halves of the muscles.

Viewed from the lateral aspect, the muscle appears as a large fan whose cranial fibres are horizontal in direction and whose most caudal fibres are almost vertical.

It has been pointed out (*loc. cit.*) that in the M. mentalis three sets of fibres could be distinguished: (*a*) medially, the arches and loops already alluded to; (*b*) lateral to these the fibres entered the skin of the chin on the same side; (*c*) caudally, in some cases there were present anomalous menti fibres. The fibrous pad and bursa were found as above described.

In the so-called cleft chin the arched fibres probably are few in number or absent and the skin of the chin will be directly adherent to the subjacent fibrous pad. In the same article it was shown that the action of the M. mentalis was that of a two-cycle pump in which the cylinder walls are represented by the fibres of the M. mentalis, the piston by the fibrous pad, and the cylinder head by the fibres of the M. orbicularis oris and the M. quadratus labii inferioris. When the cylinder walls contract the piston is forced upwards and this in turn forces upwards the cylinder head and therefore the lower lip. Incidentally the chin becomes cylindrical in shape and the skin pitted. When the cylinder head contracts the piston is forced downwards and flattened against the underlying bursa and symphysis menti. This brings about a dragging downwards of the lower lip and a flattening of the chin. It is upon this explanation of the action of the M. mentalis that the present article is based.

In describing the expression of grief, Charles Darwin states: "The corners of the mouth are drawn downwards, which is so universally recognised as a sign of being out of spirits, that it is almost proverbial" (*Expression of the Emotions*, p. 182).

This statement is selected to exemplify the current opinion with regard to the position of the angle of the mouth in distress, and to serve as a concrete basis for the discussion of this movement of the angle of the mouth.

None will doubt that the movement of the modiolus[1] determines the position of the angle of the mouth, but can the modiolus be dragged caudally by the modiolar muscles? This is extremely improbable and such movement as may take place would be so small that it could have no influence nor effect upon the facial expression. If the modiolus cannot be drawn caudally it follows that neither can the angle of the mouth be drawn downwards. Much depends upon the answer to this question, which has been approached from two aspects, the experimental and the purely anatomical. It may seem extravagant to designate as experiments the following simple procedures which are easy of application; yet their results are clear and convincing. To obviate any con-

[1] The modiolus corresponds to the "node" of Quain (Bryce, vol. IV, pt II) or the "Knoten" of Eisler, and is a mass of muscle situated between the skin and mucous membrane, and composed of fibres from all the muscles which approach the angle of the mouth (*Journ. Anat.* vol. LX, pt I, Oct. 1925).

fusion of thought or observation the movements of the angle of the mouth were observed with the teeth in apposition; afterwards the effect of the opening of the jaws upon the position of the modiolus was examined.

The unilateral downwards or caudal movement of the modiolus will be examined first as it possesses many advantages over the simultaneous depression of both modioli. In the former the excursion of the angle of the mouth is greater, the movement is more simple to perform, the impression of a downward movement of the angle of the mouth is much more decided and the contortion is more easy to examine.

When the subject has depressed as far as possible one angle of the mouth let the lower lip be everted yet further by the finger and the angle of the mouth accurately located. Opposite and perpendicular to this a pencil point is held and the mouth allowed to return to a position of rest. It will be found that the pencil point is now on the same horizontal plane as the resting position of the angle of the mouth though considerably lateral to it, and if the pencil shall have brushed against the skin of the face an horizontal or semicircular line will have been traced across the cheek. The ocular deception in the experiment was very great, for even when the angle of the mouth had been accurately defined, it appeared to lie caudal to its fellow of the opposite side and the whole of the rimal slit looked to be sloping instead of horizontal. That this is not due to an involuntary raising of the opposite modiolus can easily be proved by repeating the pencil experiment on the opposite or still side of the face. This angle of the mouth remains stationary.

The illusion is due (1) to the apparent lengthening of the upper lip upon the active side of the face due to the lateral, though horizontal stretching of the rima oris. (2) The line of the rima oris makes with the lower border of the mandible a very definite angle—if prolonged, the two lines would meet close to the angle of the jaw. Any horizontal prolongation of the rima oris would bring these two lines into closer proximity, which would give the optical illusion of a lowering of the rima oris. (3) The pars labralis platysmae does not reach laterally as far as the angle of the mouth, and when it acts vigorously it tends to create a false angle of the mouth at the point of its most lateral attachment to the lip. The false angle is lower than the true angle of the mouth and is apt to be regarded as the true angle of the mouth. (4) The same muscle when in activity everts the red lip area of the lower lip which adds to the illusion alluded to above. (5) Heightening the effect of the above is the deep skin furrow which passes close to and sometimes conceals the angle of the mouth. This is caused by the muscular and almost fat-free lower lip being dragged outwards against the surrounding panniculus adiposus.

A similar experiment made whilst the subject attempts to depress simultaneously both corners of his mouth will yield very similar results. It is less striking for the lateral displacement is less and the line traced by the movements of the angle of the mouth is shorter.

The movement of the angle of the mouth during laughter was also

examined to confirm, by contrast, the foregoing results. In laughter the line traced by the movements of the angle of the mouth is a straight line lying almost parallel but slightly medial to the direction of the M. zygomaticus. With the teeth closed it seems quite impossible to drag down the corners of the mouth and some other means must be employed by the facial musculature to give this illusion. This will be discussed later.

Finally, a test was made of the effect of opening the mouth upon the level of the modiolus and the angle of the mouth. In this case the position of the angle of the mouth when widely opened was marked by the pencil and the subsequent change and the position of rest noted and marked upon the skin. No alteration in the level of the modiolus was noted until after the "neutral" position had been passed. When the mouth opened more widely than this, the depression of the modiolus and angle of the mouth was found to vary directly as the depth of the rimal aperture, though always it remained approximately midway between the upper and lower sets of teeth.

Also it was noted that the deeper the aperture the less control the modiolar muscles were able to exercise. Next, a study of the anatomy of this region was made to substantiate these experiments and to explain the difficulties to be overcome, when attempting to depress the corners of the mouth whilst the teeth remained closed. To do this it was found necessary to study each muscle in relation to its own group and the grouping of the previous article has been retained. Briefly, this was as follows:

(1) *Muscles acting upon the modiolus:*

- (*a*) M. cruciati modioli
  - M. caninus
  - M. zygomaticus
  - M. triangularis (caput buccale, caput latum, caput longum).
- (*b*) M. transversi modioli
  - M. orbicularis oris
  - M. buccinator.
- (*c*) Portio modiolaris platysmae.

(2) *Muscles acting upon the lips, i.e. the labial tractors:*

- (*a*) M. quadratus labii superioris
- (*b*) M. quadratus labii inferioris
  - portio labralis platysmae.

(3) *Accessory muscles:*

- (*a*) M. mentalis
- (*b*) M. incisivus superior
- (*c*) M. incisivus inferior.

Of the cruciati modioli the M. zygomaticus differs in two respects from the remainder:

1. It is of much greater length.
2. Its action tends to lift the modiolus away from the teeth and gums

owing to its origin from the prominent malar bone. The other muscles of this group tend to press the modiolus against the teeth and gums.

These two points of difference give to the movements of this muscle greater flexibility and a wider range. They make the M. zygomaticus the commanding influence or sentinel muscle of this middle region of the face, and nothing short of its involuntary complete inhibition would allow unrestricted movement to the other muscles of its group.

Whether this inhibition ever occurs during a vigorous facial movement seems extremely doubtful and to test this by direct observation Miss *X* was asked to depress the corners of her mouth. Each time she attempted this the M. zygomaticus was seen in strong activity. Miss *X* is suffering from a lipodystrophy and her facial muscles can be seen when in activity. Cinematograph films of her face have already been dissected (*loc. cit.*).

It might have been inferred that if the caput longum M. triangularis were in activity the M. zygomaticus would be a very active antimere (compare the reverse of the activity as seen in the expression of the emotion of laughter). This activity of the M. zygomaticus merely might regulate rather than prevent the depression of the angle of the mouth, but there is another greater, if not insuperable, obstacle to such a depression.

During an attempt to depress the angle of the mouth, a striking feature is the eversion and the dragging laterally and caudally of the lower lip by the inferior labial tractors, especially the portio labralis platysmae, which action hides completely the true angle of the mouth. (This concealment of the angle of the mouth is due to the deep creasing caused by the muscular lip being dragged against and partly beneath the surrounding panniculus adiposus.) The powerful portio labralis platysmae lies directly beneath the muscle loop formed by the caput longum M. triangularis, and when in strong activity it forms a solid muscle mass, wedged between the modiolar mass above and the fixed bony attachment of the caput longum below. Thus it effectively prevents the caput longum M. triangularis from dragging caudally the modiolus and, as its insertion into the lower lip is medial to the angle of the mouth, the portio labralis platysmae cannot drag the angle caudally.

The true antimere to the activity of the caput latum M. triangularis would be the resultant of the activities of the M. zygomaticus and M. caninus, and this might be great enough to hamper the downward descent of the modiolus. Indeed it almost seems a necessity that this should be so, as otherwise undue pressure might be brought to bear upon the portio labralis platysmae.

A somewhat similar argument holds against the M. incisivus inferior dragging the modiolus caudally. These three muscles, capita longum et latum M. triangularis and M. incisivus inferior, are comparatively short muscles and their very shortness would restrict greatly much downward movement. Another muscle able to depress the angle of the mouth is the portio modiolaris platysmae. The action of this muscle is to drag the modiolus laterally rather than caudally and the caudal dragging is again negatived by forces

similar to, if not identical with, those just mentioned for the caput latum M. triangularis.

Thus it will be seen that a depression or dragging downwards of the modiolus would be an extremely difficult if not impossible task owing to the anatomical disposition and physiological activities of the muscles acting upon it.

The commanding influence of the M. zygomaticus upon the middle region of the face, and especially upon the position of the modiolus, seems a necessary corollary to the above-mentioned experimental and anatomical facts. Its greater flexibility and its wider range of movement, its lateral lift and the direction of its fibres makes it an efficient protector of the portio labralis platysmae from undue pressure by the other modiolar muscles just mentioned. It might be called the sentinel muscle of the middle region of the face. Thus, ever on the alert, it becomes the medium for the expression of man's commonest emotion, namely, joy and high spirits.

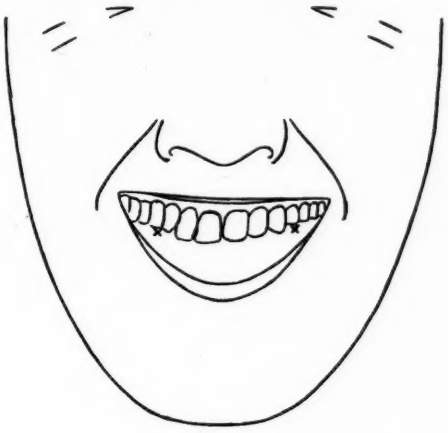

Fig. 1. Laughter.

A recapitulation of the muscular activities during laughter and the effects caused by them will be given before describing distress, as it affects the lower half of the face. This will afford not merely a foil but a basis on which to build.

*Laughter* (fig. 1). The mouth is widely opened and the teeth separated. The modioli are drawn cranially and laterally and the upper lip forms a straight or slightly orally convex line stretching from modiolus to modiolus. This exposes the upper teeth as far laterally as the 1st molars and cranially as far as the gingiva or even this may be exposed. The distance between the nasal septum and the "red" margin of the upper lip is very much decreased, the nasolabial fold is deepened, concave oralwards, extended caudal to the rima oris and its cranial portion is more horizontal in direction. The lower lip is bowed downwards with a very marked oral concavity, but the lower teeth are only

slightly exposed, or they may not be seen. This marked semilunar outline of the lower lip is due to three causes: (1) the cranial position of the modiolus; (2) the caudal position of the mandible; (3) the activities of the inferior labial tractors.

The muscular activities which cause laughter are:

Modiolar muscles: The M. zygomaticus is dominant and the caput longum M. triangularis is resistant.

Labial muscles: The superior and inferior labial tractors are dominant—the M. orbicularis oris is completely and involuntarily inhibited. It is this inhibition which is the basis of true laughter.

*Distress.* The examination of the antitheses of laughter has many obstacles, the chief of which is the difficulty of its voluntary reproduction. Even had this difficulty apparently been overcome may not the result have been similar in its dissimilarity to "forced laughter" (*loc. cit.*)? The next difficulty is the answer to the question: How is distress expressed? That facial expression of itself is not sufficient is easily understood if one peruse such illustrations as may be seen in Dante's *Divine Comedies*, whether by Gustave Doré, Botticelli or by Blake, when it will be realised how little the artist relies upon the facial expression and how greatly upon the expression of the body musculature. The headless body writhes and nauseates us with its pain and often with the face concealed the attitude of body reveals to us the attitude of mind.

Then again, all are familiar with the erect figure of joy and high spirits, the drooping figure of grief, the clenched fist of rage and many other attitudes of face and body due to the activity of the mind when under the influence of the various emotions. But is the converse never true? Do the experiences of the body never influence the mind? do they never cause an attitude of body and a facial expression indicative of these experiences quite apart from any psychological effect or influence? In other words, may not a similar facial signal be hoisted, as it were, by mental distress due to unhappy news or grievous thoughts, and by combined mental and physical distress such as may be caused by pain and by purely physical distress due to great physical strain? The latter has been most admirably depicted by Prof. R. Tait Mackenzie, *Journal of Anatomy*, vol. XL, pp. 51–6. The resemblance to pain or grief in the expression of the breathless or distressed runner is unmistakable and the following picture of fatigue might equally well represent sorrow. Thus it appears that not only do emotional disturbances cause activity of all the muscles of the body as well as of the facial musculature, but that stress or distress of the body causes a stimulation of the emotional receptors in the brain which varies as the energy expended and the capability of the body to perform its task. The result of this is reflected in the facial expression which often assumes some recognisable form of emotion. This is too large a question for this article and distress as an emotion will be considered only. Again, is the expression of distress like that of laughter, a password common to all races and at all ages of growth, or do different races or different ages in the same race express them-

selves in different ways? That the lamentations, the behaviours and the distress of grief-stricken peoples differ very widely, gives us no information as to the facial expressions, and it were better to consider only those people with whom one is brought in close contact.

Do people of Anglo-Saxon or allied temperament express their distress differently in any part of their seven ages? The answer seems undoubtedly in the affirmative. There seems to be an ontogenetic development of the expression of distress, probably corresponding to the phylogenetic, and depending upon the stage of development and age of the individual. The child cries much as the kitten mews or the lamb bleats, the school-boy endeavours to hide not only his tears but his emotions, and the adult almost accomplishes his school-boy desires. Some classification of the various phases of this emotion has been attempted, and is as follows:

*Distress:* A. Primitive or Simple.
B. Associated or Complex.
(*a*) Expressed:
1. Reserved.
2. Unreserved (Hysterical).
(*b*) Masked:
1. Repressed (Hysterical).
2. Controlled.

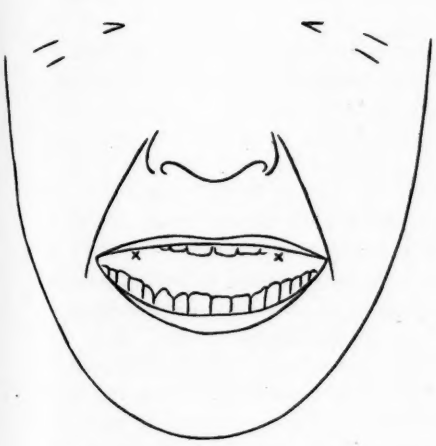

Fig. 2. Primitive or simple distress.

Fig. 3. Similar to Fig. 2 but more vigorously expressed.

A. *Simple distress* (figs. 2 and 3) is usually to be seen in infants and young children, and is due to bodily discomfort not amounting to pain. Hunger, tiredness, or the feeling of coldness, whether due to insufficient clothing or a wet napkin, will readily evoke this response. To the child or infant these are

calamities yet they are not of a nature to arouse any emotion of fear. It is a primitive response to a simple stimulus and in this respect is the true counterpart of laughter and probably, like laughter, its expression is indicated by and depends upon a complete involuntary inhibition of the M. orbicularis oris. In the wailing of infants (fig. 2) the modioli are drawn laterally and the upper lip is bowed slightly upwards. This gives a relative lengthening of the lateral portions of the upper lip and an apparent descent of the modioli; it also exposes portions of the central incisors (when present). The naso-labial folds extend caudal to the rima oris, are almost straight, approach the vertical and pass very close to the angles of the mouth.

The lower lip is bowed caudally, exposing the crowns of any teeth that may be present.

The muscular activities which give expression to simple distress are:

Modiolar muscles: The portio modiolaris platysmae and capita longum et latum M. triangularis are dominant and the M. caninus and M. zygomaticus resistant. The caput buccale probably is not acting (cf. laughter).

Labial muscles: The inferior and superior labial tractors are dominant. The M. orbicularis oris probably is completely and involuntarily inhibited.

A more vigorous infant might roar at his discomforts and this is shown in fig. 3, and is but an exaggeration of the previous picture. The mouth is more widely opened and this brings the modioli a trifle closer to the median plane and lowers them to a position midway between the upper and lower dental arches.

In simple distress the M. mentalis is not called upon to act during the expiratory phase of the emotion. The expression assumed by the mouth in simple distress is not a very distinctive one and might be mistaken for amusement or laughter were it not for the accompanying signs of grief, either in the brow or general attitude of the subject. Such a criticism has been levelled at one of Darwin's classical pictures of an infant crying (*op. cit.* Plate I, figs. 1 and 2), which Prof. Cleland has remarked is very much akin to that of an old man roaring with laughter. In this respect it is well to remember that the photograph is taken at an oblique angle. It is also interesting to compare this photograph with fig. 1, and with the description of a maudlin alcoholic's grief given under the next heading (reserved associated distress).

But in distress as in all emotions there are waves of intense, alternating with periods of less emotional stress and in a vigorous effort, such as depicted in fig. 3, there must be pauses to take breath.

In each of these temporary remissions the M. mentalis will be seen to act with great vigour even in very young infants. It is the quickest way of closing the rima oris and is made use of when attempting to control or conceal distress. Like the legendary ostrich, that covered its head with sand to conceal its body, man thinks to conceal his emotion by covering his oral cavity with his lips.

This simple weeping or roaring is seen depicted in comic papers, but it is drawn often with a straight lower lip and much depressed angle of the mouth.

B (*a*) 1. *Reserved Associated Distress* (fig. 4) is so called, because the weeping is generally secondary to some ineffective or frustrated desire or some strong emotion such as joy or anger.

The child endeavouring to control his tears, the spoilt child screaming because he cannot get his own way and the person weeping with joy or anger, all present the common feature of a vigorously acting M. mentalis. The two latter are complicated by an association with emotions other than distress, yet the suggestion of distress is conveyed by the action of the M. mentalis in altering the outline of the lower lip and causing the chin to appear swollen, pitted and roughened. In the cases of the children cited above, the mouth of each assumes a somewhat similar shape, which has been described by Charles Darwin (*op. cit.* p. 152), "give to the mouth an oblong almost squarish outline."

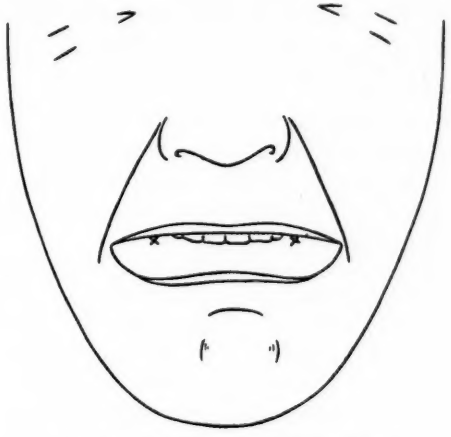

Fig. 4. Reserved Associated Distress (B (*a*) 1).

Darwin regards these movements of the "commissure" as due to the M. depressor anguli oris (M. triangularis), but the "accompanying photographs" all show a most vigorously contracted M. mentalis. In reserved associated distress (fig. 4) the mouth is slightly or moderately opened and the teeth separated. The modioli are drawn laterally and may be slightly caudal to the position of rest. The upper lip is slightly concave orally, exposing slightly the upper teeth and the red lip may be unevenly and more exposed than usual. The distance between the nasal septum and the red lip is considerable and the nasolabial fold is almost straight, approaches the vertical, passes close to the angle of the mouth, and extends caudal to the rima oris. The lower lip is dipped laterally, but elevated medially and no teeth are visible. The powerful M. mentalis is able to overcome in the middle area of the lip the downward pull of the labial tractors, but the portions of the lips lateral to its influence remain

markedly bowed. This forms a false angle of the mouth and gives the impression of a turning down of the corners of the mouth (*vide* Froriep figure, p. 51). The true angle of the mouth is close to the nasolabial fold and is not lowered more than is consistent with the amount of opening of the jaws.

The muscular activities causing this are:

Modiolar muscles: The portio modiolaris platysmae and capita longum, latum and buccale M. triangularis are dominant and the M. caninus and M. zygomaticus resistant.

Labial muscles: The superior and inferior labial tractors are dominant and the M. orbicularis oris is resistant. This latter muscle no longer is inhibited involuntarily and in consequence we get the caput buccale M. triangularis in activity.

It might be well here to relate the facial expressions observed in a "maudlin drunk" man, who was clean shaven, or at least had been two days previously. After a short quiescence, his mouth was opened moderately, the lips slightly separated, the angles of the mouth raised and there was no sign of activity of the M. mentalis. The expression of the mouth was similar to fig. 2 and might have been mistaken for a smile had it not been for the grief-stricken brow. This condition remained for 15 to 20 seconds and then tears showed in the eyes. Immediately after this the M. mentalis came powerfully into action and the mouth became as expressive of distress as the forehead. The resemblance to fig. 4 now was most marked.

Reserved associated distress is seen occasionally in black and white drawings, and two representations of it were found in pictures in the Art Gallery at Sydney. In each of these latter the shape of the mouth was similar to fig. 4, and there was a marked swelling of the chin which denoted a vigorously acting M. mentalis. The Laocoon group is represented in the same gallery by a very fine plaster cast of the original, and in each of the three figures the above-mentioned points are well depicted. This is the more extraordinary as the central figure is a bearded one.

B(*a*)2 and B(*b*)1. *Hysterical Distress.* Here tears and laughter may follow each other in quick succession and the facial expression is ever inconstant.

B (*b*) 2. *Controlled Associated Distress* (fig. 5). This mode of expression of distress is seen usually in adults and is due to their habitual suppression of emotion. It is seen also in children just when they have mastered their weeping. This latter type has been described by Darwin (*loc. cit.*) as follows: "When the mouth is closed...the commissure or line of junction of the two lips forms a curved line with the concavity downwards, and the lips themselves generally are somewhat protruded, especially the lower one." He ascribes this to the M. depressor anguli oris, but his photographs again show undoubtedly a very vigorous M. mentalis in each case.

In adults this picture is accentuated, since their desire to hide their emotion is much stronger and their long continued suppression and repression aid them to effect this. Fig. 5 represents great stress, but also great control. Should

the stress be pushed to the limit of control, the facial expression would resemble Duchenne's photograph which he labels discontent or contempt. The close resemblance of repressed laughter to this picture has been noted elsewhere (*loc. cit.*). In controlled associated distress the mouth is firmly closed and for this reason the position of the angles of the mouth is hard to determine. They are firmly fixed by the cruciate and accessory modiolar muscles and may lie slightly medial and cephalad to the position of rest or remain fixed in the position of rest. The rima oris is reduced to a narrow cranially bowed slit apparently extending caudal to the modioli. The explanation of these appearances is as follows: the modioli are fixed and the superior and inferior portions of the M. orbicularis oris strongly contracted. The M. mentalis is acting vigorously and pushing the lower lip more firmly against and slightly underneath the upper lip. This obliterates the lateral portions of the red lip and

Fig. 5. Controlled Associated Distress (B (*b*) 2).

causes the lateral portions of the upper lip slightly to overhang the lower lip. The M. mentalis also broadens laterally the whole of the lower lip and pushes this muscular and almost fat-free organ against the panniculus adiposus, thus causing a very marked lateral creasing, more or less continuous with the curved depression of the rima oris.

The nasolabial folds become straight and almost vertical in direction—they do not extend caudal to the rima oris and lie lateral to the angle of the mouth. (Very few illustrations of repressed distress could be found in the pictures that were available. A good example of it is a drawing by Bernard Partridge in *Punch*, 21 March, 1906, p. 201.)

The muscular activities which give expression to controlled associated distress are:

Modiolar muscles: All the muscles which gain insertion into the modiolus are in a state of extreme tension; the M. incisivus inferior and the M. triangularis probably are dominant.

Labial muscles: The M. orbicularis oris is dominant and the superior and inferior labial tractors resistant.

Accessory muscles: The M. mentalis is dominant to the inferior labial tractors and M. orbicularis oris.

## SUMMARY

1. In infants and young children the M. mentalis is used only to end a bout of weeping.

2. In older children and adults the M. mentalis may be used for this purpose. It is more commonly used to prevent an outburst of weeping since convention discourages the display of any emotion in public.

3. The piston-like action of the M. mentalis firmly presses together the two lips and bows cranially the rima oris, at the same time it broadens laterally the lower lip, pressing it under the panniculus adiposus and produces a marked creasing lateralwards.

4. This lateral creasing extends from the angle of the mouth caudal and laterally and continues the curved depression of the rima oris.

5. This gives the impression that the angle of the mouth has been dragged caudal and laterally, which movement was supposed to be accomplished by the M. depressor anguli oris. This article has attempted to show that when the rima oris is closed there is no depression of the angle of the mouth.

6. By stiffening the lower lip the M. mentalis assists man to control emotion. This is contrary to the adage which enjoins a stiff upper lip.

The bibliography used for this article corresponds with that used for the article in the *Journal of Anatomy*, October 1925.

I am much indebted to Dr Gavin Morton for the exhibition of many insane people suffering from melancholia, to Prof. Burkitt of the Anatomy Department, Medical School, Sydney University, for perusal of the article and suggestions, to the Anatomy Department of the same Medical School for material and use of its laboratories and to the Staff for many acts of courtesy and assistance. Also to Dr H. T. Lovell, Professor of Psychology, for assistance in the classification of the various forms of distress, and to Mr H. M. Green, M.A., chief librarian, who assisted me greatly, and amongst other books procured *Der Ausdruck des Menschen*, by Heinrich Rudolph.

In addition the *Anatomie für Künstler*, 1921, by Dr August von Froriep was consulted.

# MULTIPLE MALFORMATIONS OF THE LIMBS

By J. A. PIRES DE LIMA, M.D.

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Dubreuil-Chambardel(1) classifies variations of the fingers and toes into six groups, as follows:

I. Variations in the number of digital rays: increase—*hyperdactylia*; decrease—*hypodactylia.*

II. Variations in length of the digits, the number of the phalanges being normal: increase—*megalodactylia*; decrease—*brachydactylia.*

III. Variations in volume of the digits: increase—*macrodactylia*; decrease—*microdactylia.*

IV. Variations in the direction of the axes of the digits (*clinodactyly*): antero-posterior deviations—*camptodactyly*; lateral deviations—*varus* or *valgus.*

V. Variations of the phalanges: increase—*hyperphalangism*; decrease—*hypophalangism.*

VI. Variations affecting the independence of the individual digits: *syndactylia.*

In a book recently published(2) I showed that pure anomalies can be seldom classified by means of the foregoing scheme, as, in most cases, several variations are associated not only in the same individual but also in the same limb. In this book I have recorded 70 cases of congenital atrophies of the limbs occurring in Portuguese and have shown that these deformations are much more frequent in the male (67·1 per cent.) than in the female (31·4 per cent.). In other words, more than two-thirds of the persons affected by congenital atrophy of the limbs were males.

I noted further that, as a rule, two, three or more anomalies were associated in the same individual and that these anomalies occurred most frequently at the distal extremities of the four limbs (22·8 per cent. of all cases).

Since my book was published I have had the opportunity of observing some further cases of limb anomalies and a description of the most remarkable of my hitherto unpublished cases, which came under my notice on the 6th May, 1927, may prove of interest.

Ernesto A. P. R. of Oporto, a male 7 years old, in addition to malformations of the four extremities has very deformed ears which are cornet-shaped and inclined forward (fig. 1). One of his brothers was born nearly deaf and as a result his speaking is faulty.

The right hand of my case is greatly atrophied and reduced to a thumb, the skeleton of which is represented by a very small phalanx (figs. 2 and 3).

A radiograph of the hand shows no trace of carpus, of metacarpus, or of digits other than the thumb.

The left hand is affected by brachydactyly due to atrophy of the intermediate phalanges, as is clearly visible in the radiograph (fig. 3). In addition to the agenesis of the trapezoid or of the capitate bone the three ulnar digits of the left hand are camptodactylous and the third metacarpal bone exhibits a forward bend.

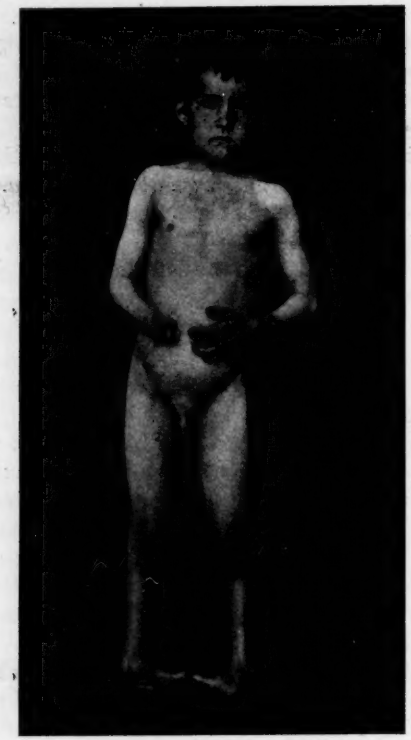

Fig. 1.

Both feet are affected by club-foot of the varus type (fig. 4). In the right foot (figs. 4 and 5) the calcaneus is well developed but has suffered a congenital luxation and a considerable displacement, being nearly vertically disposed with the posterior surface opposed to the distal extremity of the fibula.

Below the calcaneus and at right angles to it is a long bone which is apparently the fifth metatarsal; it supports a rudimentary toe (? fifth toe) exhibiting two phalanges and incapable of active movement.

Fig. 2.

Fig. 3.

The distal part of the foot consists of a well-developed transversally disposed hallux, with the first metatarsal. Proximal to the first metatarsal are two nuclei which may represent the first and second cuneiforms. Between the calcaneus and the epiphysis of the tibia are two little nodules which cannot be identified. It is to be noted that in this foot there is agenesis of the talus.

The left foot is also greatly deformed and transversally disposed with the free extremity of the hallux looking towards that of the right hallux (figs. 1 and 4). In this foot there is also agenesis of the talus; the calcaneus is vertically disposed and overlaps the lower end of the fibula. In addition to the calcaneus, which is small and not so well developed as the corresponding

Fig. 4.

bone of the right foot, the following osteological elements are present (fig. 6). A deformed first metatarsal, at the distal extremity of which are the elements of two toes, a fairly well-developed hallux and a minute nailless toe represented by a phalanx only. This rudimentary toe is situated below and on the fibular side of the hallux. Between the proximal extremity of the first metatarsal and the inferior tibial epiphysis may be seen two little osseous nodules, which probably represent the first cuneiform and the navicular. In the neighbourhood of the distal end of the calcaneus is a small elongated nodule, which may represent the terminal phalanx of another toe (? fifth).

The bifid left hallux may be regarded as a compensation for the absence or extreme atrophy of the fifth toe, which is better developed in the right foot but reduced to a phalanx in the left.

As the talus is absent and is not interposed between the tibia and the

Fig 5.

Fig. 6.

calcaneus in both feet the latter bone has assumed a vertical position. At the same time, the reduced elements of the fore part of the foot, the metatarsus and the toes, have suffered an inward rotation of 90° and the outer sides of the two feet, which thus look forwards, function as the chief pedal supports.

In spite of the deformities of his feet the boy can walk quickly, with the knees far apart, the feet transversely disposed and the trunk oscillating from side to side.

(Radiographs by Dr Roberto de Carvalho.)

## LITERATURE

(1) Dubreuil-Chambardel. *Les variations du corps humain.* Paris, 1925.
(2) J. A. Pires de Lima. *Anomalias dos membros nos Portugueses.* Porto, 1927.

# NOTES ON THE HISTOLOGY OF THE OVIDUCT OF THE DOMESTIC HEN

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The following notes are meant to be regarded as no more than an addendum to a comprehensive account of the histology of the oviduct of the domestic hen given by Frank M. Surface in 1912[1]. The investigation, of which they may be taken as a report, was undertaken chiefly because Surface himself suggested that certain points would bear further enquiry.

In all, fourteen oviducts have been examined; but half of these have been used for purposes of comparison only, and this because uniform methods were not followed in their preparation. Seven oviducts, on the other hand, all taken from hens in full laying activity, were fixed and prepared in precisely the same way. The material was fixed in Susa's formaldehyde-corrosive-sublimate solution, passed through the alcohols and carbon tetrachloride, and embedded in paraffin.

*Infundibulum.* In his description of the infundibulum, Surface gives a very clear account of the folds of mucous membrane present in this part of the oviduct, and of the epithelium that covers the folds. He distinguishes two kinds of epithelial cells, namely, ciliated and non-ciliated; the former covering the more superficial part of the folds. The non-ciliated cells are limited to the deeper part of the grooves between the folds, and are regarded by Surface as being glandular in character; the "glandular grooves" or "gland pouches" they line being the precursors of the true tubular glands of the succeeding albumen-secreting part of the oviduct. Surface also points out that as the infundibulum merges into the albumen region, other non-ciliated cells—to which he applies the term "unicellular glands"—make their appearance among the ciliated epithelial cells.

My own observations go to confirm Surface's statements in every particular. But certain staining reactions make it possible to add that Surface's "unicellular glands," which will be referred to in future as goblet cells, produce a secretion that, from its staining properties, must be looked upon as either mucin or something akin thereto. Bismarck brown and neutral red stain it readily, and thionin blue—usually regarded as a specific differential stain for mucin—colours it pink. From Mallory's stain it selects the blue.

[1] "The Histology of the Oviduct of the Domestic Hen," *Ann. Report, Maine Agric. Exp. Station*, 1912, pp. 395–430, 5 plates (Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 40).

Because of what is observable in the albumen-secreting portion of the oviduct, it is worth noting that the differentially stainable material occupies a comparatively small part of the cell in the infundibulum. It is also worthy of note that the cells of Surface's "glandular grooves" or "gland pouches" do not give the staining reaction displayed by the goblet cells.

In brief, the epithelium of all but the earliest part of the infundibulum contains three different kinds of cells: (*a*) ciliated, (*b*) goblet cells, and (*c*) non-ciliated cells that are not goblets. The last-named occupy depressions that may not unreasonably be regarded as the forerunners of the tubular glands of the succeeding part of the oviduct; but it would not be consistent with their microscopic character to look upon the depressions as in any way functionally similar to the albumen-producing glands. Each cell lining them is cuboidal in form, with a nucleus that occupies about half the height of the cell, and a cytoplasm that contains none of the granules that are so characteristic of the true albumen glands.

Nevertheless there are reasons for considering that the depressions are the first step towards the formation of real glands. An examination of a series of sections of the region of mergence of the infundibulum into the albumen-secreting portion of the oviduct tempts to this view. In such a series the depressions become gradually deeper and finally assume the form of real tubules. As the tubules take on a more and more definite form, the cells lining their deeper part increase in size and fine granules appear in their cytoplasm; or, in other words, the epithelium gradually becomes specialised and assumes the characters of that of the albumen-secreting glands. The part of the tubules nearest the surface of the mucous membrane becomes the duct of the rudimentary gland, the cells lining it retaining the primitive characters of the epithelium of Surface's "glandular groove." Fig. 1 is a diagram constructed from the appearances noted in a series of sections of the region now under consideration.

*Albumen-secreting region.* Surface describes and figures the epithelium of the tubular glands of this part of the oviduct as containing large granules, but states that large granules were absent in the deeper parts of the glands he examined—an absence that he thinks may be due to the action of the fixing fluids he employed. Available material has permitted the examination of the glands before, after and during secretion; and in no oviduct examined have granules anything like so large as those figured by Surface been found. On the contrary, the granules have invariably been relatively small; and this has been particularly notable when they have been compared with secretion granules in a later part (isthmus) of the same oviduct.

According to Surface's description, the albumen-secreting region is covered by an epithelium in which there are two kinds of cells—ciliated and non-ciliated unicellular glands (goblet cells). The nucleus of the ciliated cell is nearly always about the middle or towards the free end of the cell. The nucleus of the goblet cell, on the other hand, is more deeply situated; and the more

superficial part of the cell presents an alveolar structure. Whether the alveoli represent the gland granules or an intergranular network, Surface does not feel in a position to say. He asks whether the goblet cells differ in the character of their secretion from the cells of the tubular glands, and, because of certain staining peculiarities, concludes that they do.

An examination of the whole length of the albumen-secreting portion of the oviduct leaves no escape from the conclusion that the goblet cells are of considerable importance. They are very numerous—quite as numerous as the ciliated cells—and of great width. Even in the infundibulum, the ciliated cells

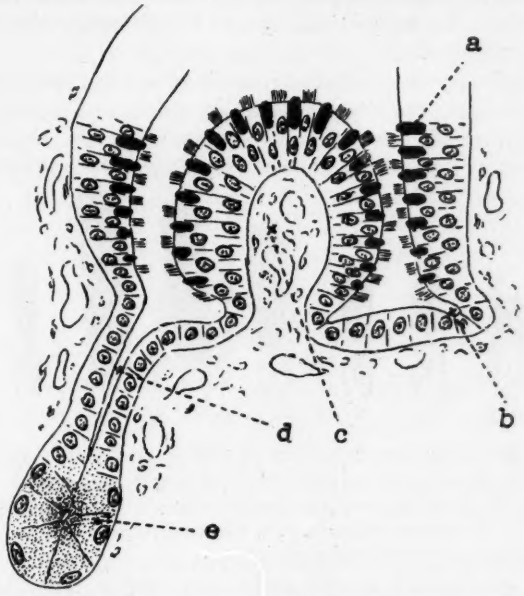


Fig. 1. Diagram of the region of transition from infundibulum to albumen region. *a* = goblet cell; *b* = Surface's "glandular groove"; *c* = small fold of mucous membrane; *d* = duct of rudimentary albumen gland; *e* = secreting part of rudimentary gland.

are narrower than the goblets; and in the albumen region the disparity in width gradually becomes more and more marked until, in the last part of the region, the ciliated cells are so much compressed that, except where the nucleus occurs, they appear in sections as little more than lines. Or, stated in terms of function, the last part of the albumen region is practically a continuous mucin-secreting surface.

In the early part of the albumen region the goblet cells are neither notably tall nor remarkably wide, and the material they produce does not occupy much more than about half of their interior. There is, however, a conspicuous increase in both their height and width as the junction of this region with the isthmus

is approached. Concurrently with the increase in the volume of the cell there is an even more than commensurate increase in the amount of secretion each cell contains when fully loaded. This will be apparent if the outline drawings given in fig. 2 are compared. It will also be observed that, owing to the augmentation in the amount of the secretion, the nucleus is finally displaced to and compressed at the deep end of the cell.

The secretion of the goblet cells gives the pink reaction with thionin blue that is usually considered to be characteristic of mucin. It also stains deeply with Bismarck brown and neutral red, and is blue in sections treated with Mallory's fuchsin-orange-anilin-blue stain. It has been found that Bismarck brown and neutral red are particularly useful in demonstrating the granular nature of the secretion.

One, in particular, of the oviducts examined was of considerable interest. It contained an egg in the albumen-secreting region; and sections of the wall of the duct with the adjacent layer of the white of the egg, when stained with Bismarck brown or neutral red, showed very clearly the process of extrusion

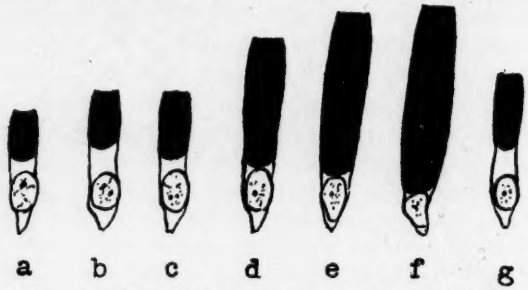


Fig. 2. Camera tracings of goblet cells from different parts of the oviduct to show their relative size and the amount of secretion (black) they contain. *a*=infundibulum; *b*=junction of infundibulum and albumen region; *c, d, e, f*=successive parts of the albumen-secreting region; *g*=junction of albumen region and isthmus.

of the mucin or mucoid from the goblet cells. The secretion is apparently extruded in the form of large droplets that, immediately they become free, disintegrate into fine granules and lose the characteristic staining reaction with thionin, Bismarck brown and neutral red. This is scarcely consonant with the description of the process as given by Surface, who says: "In sections taken where a yolk is descending, the secretion from these glands (goblet cells) can often be seen pouring out in little streams from each cell." The appearance in sections of the oviduct just mentioned certainly does not suggest "streams."

The study of sections of egg-containing oviducts produces the feeling that a fuller enquiry into the process of formation of the various constituents of the white of egg is desirable.

*Isthmus.* As is well known, the albumen-secreting region terminates at a narrow zone devoid of glands and, consequently, is distinguishable by the naked eye because of the relative translucency of the wall of the oviduct at

this point. Surface has noted that the epithelium here contains the two kinds of cell that occur in the preceding region; and to his description little need be added. The goblet cells react to stains in the same manner as the similar cells of the adjacent albumen region, but they are much smaller and contain much less secretion or, stated in another way, they resemble the goblet cells at the junction of the infundibulum and albumen region.

Surface asserts that in the isthmus itself, ciliated and goblet cells are present and that they have the same appearance as those of the albumen region in a similar state of activity. That the two kinds of cell are present is undoubted, but they differ in height and in other respects from those of the preceding part of the oviduct. In height they are not, on the average, very much taller than those of the infundibulum. This will be evident by a glance at fig. 3, in which the height of the epithelial cells in different regions has been represented against an ordinary 0·01 mm. stage micrometer scale. It should be added that in this diagram no attempt has been made to indicate differences in the width of the cells.

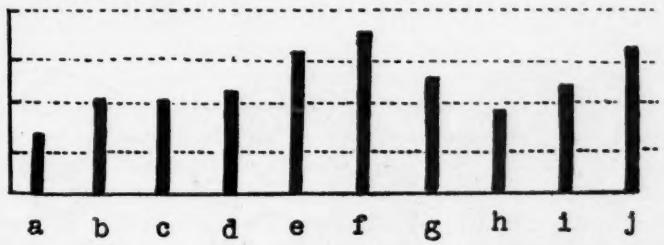


Fig. 3. Diagram to show the height of the epithelium in different parts of the oviduct. *a* = infundibulum; *b* = junction of infundibulum and albumen region; *c*, *d*, *e*, *f* = successive parts of the albumen-secreting region; *g* = glandless junction of albumen region and isthmus; *h* = isthmus; *i* = uterus; *j* = vagina.

But the most striking peculiarity observed in the epithelium of the isthmus is the behaviour of the goblets towards various stains. With Mallory's stain the mucin or mucoid colours a pale blue; but, with an exception to be noted later, it gives no notable reaction with thionin, Bismarck brown or neutral red. This circumstance seems to make unavoidable the conclusion that whatever the nature of the secretion of the goblet cells of the isthmus may be, it is not precisely the same as that of corresponding cells in earlier parts of the oviduct. It may ultimately be possible to find some reagent that will clearly and sharply differentiate the cells in the different parts of the duct, but so far search has been vain.

As already stated, the granules in the epithelium of the glands of the isthmus are larger than those of the albumen region. They are readily demonstrated by acid fuchsin, thiazin red, and eosin. The size and abundance of the granules afford a very clear and ready means of distinguishing the glands of the isthmus from those of the uterus, and enabled one to determine that there is no

definite histological boundary between these two parts of the oviduct. In sections taken in the region of their junction, both kinds of gland occur in the same fold of mucous membrane. In one oviduct, in particular, small groups of isthmus glands were found at some distance from the point at which, from naked-eye appearances, the uterus would be regarded as having begun.

It is perhaps worthy of note that, where the two varieties of gland occur together, the surface epithelium is different. Over patches of isthmus glands it resembles that of the isthmus; while in the surrounding area it has the characters of uterus epithelium.

Not only are the two glands to be found in the same fold of mucous membrane, but the examination of a considerable number of sections has led to the suspicion—amounting practically to certainty—that cells with the characters of those of the isthmus and those of the uterus may occur in the same gland. In fig. 4 sketches are shown of transverse sections of three glands that occurred within a short distance of each other. The first (*a*) contains cells all of which present the highly granular character of the gland cells of the isthmus; (*c*) has cells that are just as distinctive of the uterus glands; while (*b*) contains both kinds of cell.

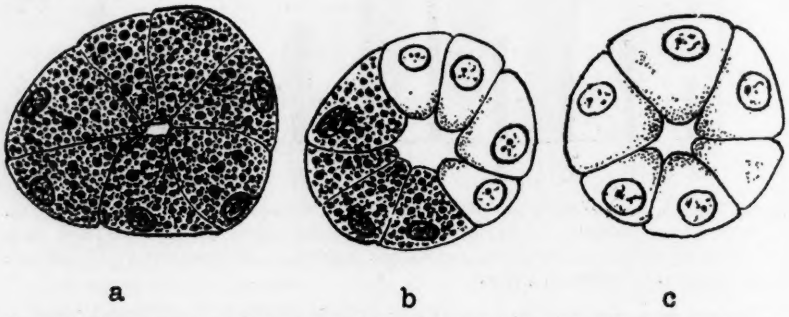


Fig. 4. Transverse sections of three gland tubules from the junction of isthmus and uterus. *a*=typical isthmus-gland tubule; *b*=mixed tubule; *c*=typical uterus-gland tubule.

*Uterus.* Inasmuch as it is composed of ciliated and non-ciliated cells, the epithelium of the uterus is like that of the rest of the oviduct. Nothing need be added to Surface's description of the ciliated cells; but the non-ciliated (goblets) present puzzling features. They are narrower than the cells that bear cilia, and throughout the greater part of the uterus efforts to produce a differential staining reaction have failed. In respect of staining reaction, the goblet cells of most of the uterus are like those of the isthmus. It has been found, however, that in the part of the uterus that immediately adjoins the isthmus, as well as in the neighbouring part of the isthmus itself, *prolonged* immersion in Bismarck brown or neutral red results in a staining effect similar to that procurable in the albumen region, and an indefinite pink coloration has been produced by allowing sections to remain in thionin for some time; but it has

been found to be impossible to retain the pink during the process of dehydration.

The ease with which a reaction can be produced in the albumen-secreting region, even by dilute stains, and the difficulty that there is in effecting a reaction in the uterus, was strikingly contrasted by staining together sections from both regions of the same oviduct, prepared in precisely the same way, and examining them at short intervals.

In describing the cells of the tubular glands of the uterus, Surface states that their nuclei are larger and more regular in shape than those in the gland cells of the albumen region, and that they lie towards the centre of the cells. He adds that the cytoplasm of the gland epithelium has a diffuse and finely granular appearance. The nuclei are certainly rounder than those of either the albumen region or the isthmus, but they usually lie in the deeper part of the cell They differ from the corresponding nuclei of other parts of the oviduct in their lighter staining; that is, in the relatively small amount of chromatin they contain. The most characteristic feature of the cytoplasm is the comparative difficulty that is experienced in demonstrating its finely granular nature.

Surface figures the secreting cells of the uterus glands as coming practically to the surface of the mucous membrane; or, as he expresses it, "the gland cells appear to force their way through the epithelium." Such an appearance as that he figures has occasionally been observed; but in some of the depressions that are present on the surface of the folds of mucous membrane a reduction of the nuclei to a single layer has been noted, and little doubt is felt that such depressions constitute the true ducts of glands.

*Vagina.* The vagina has no glands in the ordinary sense of the word. Its mucous lining is richly folded, and the surface of each fold is marked by closely set parallel grooves running in the direction of the fold. The epithelium contains ciliated and non-ciliated cells similar to those in the rest of the oviduct, and nearly as tall as the tallest of the cells of the albumen-secreting region (Fig. 3). According to Surface, the cells in the depressions between the folds are shorter, and, at the bottom of the depressions, there are frequently accumulations of what appear to be gland cells. In my own sections the epithelial cells in some places may be a little shorter, but the difference in height is very trifling and there is nothing that really suggests that they are materially different from the cells of the rest of the epithelium.

The secretion of the goblet cells is characteristically stained with thionin and the other dyes previously mentioned, but the depth of the colour is less than it is in the albumen region. In one of my specimens a part of the wall of the cloaca is included in the same section as the vagina, and it is interesting to note that the staining response of the vaginal goblets is decidedly less intense than that of the cloaca goblets. This feature may have some significance as indicating that the secretion of the goblet cells of the vagina is not identical with that of the similar cells of the intestine. Indeed, if response to stains may be taken as a guide, it is possible to go further and say that the secretion in different parts of the oviduct is different.

# ON THE QUESTION OF THE INTERPRETATION OF THE STRUCTURAL FEATURES OF THE EARLY BLASTOCYST OF THE GUINEA-PIG[1]

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Dr Norman Maclaren has recently made public some of the results of his reinvestigation of early phenomena of the development and implantation of the blastocyst of *Cavia* (1). The nature of his conclusions has induced me to re-examine critically the statements of various observers respecting the structural characters of the blastocyst of this Rodent, during the earlier phases of its development.

Since the appearance of Bischoff's monograph on the subject in 1852 (2) a number of workers have made contributions to the problem but their conclusions have been more or less discordant.

For the purposes of this paper it is unnecessary to review in detail the literature of the subject. The previous literature of early Rodent development has been analysed by Selenka (3) and, after him, in greater detail by Duval (4), in their now classical memoirs. Comprehensive lists of references to the later literature are available in Hertwig's *Handbuch* (5) and in the quite recent work of Grosser ((6), 1927).

Duval has pointed out that, in a communication appearing in September, 1882, Fraser (7) was the first to recognise that "inversion of the germ layers" is a feature common to various other Rodents besides the Guinea-pig. The same conclusion was reached independently and almost simultaneously by Selenka (3) in a publication which appeared a few months later.

To the latter author we also owe the knowledge of the absence in *Cavia* of a completed entodermal yolk-sac layer.

Thus far no general explanation of the phenomena of inversion had been forthcoming, but the solution of this general problem was fully worked out in Selenka's subsequent memoirs of 1883 and 1884.

This solution, in the case of the Mouse and Rat, was fully confirmed by the later studies of Duval and has ever since held the field so far as the latter types are concerned.

The condition in the Guinea-pig, however, shows some divergence from the otherwise closely related type of the Muridae.

As already stated, Selenka found that in *Cavia* a complete vesicular, entodermal, yolk-sac wall is not constituted. Only a proximal "visceral" layer

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of ("inverted") entoderm covering the central ectodermal cylinder is present. Later this becomes a conspicuous columnar layer. No one has succeeded in demonstrating the existence, at any period, of a distal or "parietal" entodermal layer representing an entodermal lining of the parietes of the cavity within which the amnio-embryonic cylinder is inverted.

Even in the Muridae such a distal entodermal layer is very inconspicuous and sometimes more or less imperfectly formed.

Nevertheless in them it is for a time clearly recognisable as a cellular lining to "Reichert's membrane," as Selenka's and Duval's figures show. Its presence is indeed easily verifiable at any time in suitable sections. But it appears to be totally absent in *Cavia*.

There can be little doubt that this entodermal deficiency in the latter case must be correlated with the fact that in this type no Reichert's membrane is formed. The presence of any other representative of the original trophoblastic wall of the blastocyst is at best so difficult to establish that its real existence is strenuously denied, as we shall see, by some observers.

Selenka, however, quite definitely maintained the objective reality of such an outer layer of (trophoblastic) ectoderm ("hinfälliges Ektoderm," auct.). In various figures of Taf. XI of his 1884 memoir ("Die Blätterumkehrung," etc.) he shows it as a quite recognisable, though faint and impermanent, layer.

A like view was adopted by Duval although in this instance it was unsupported by other than schematic figures.

Selenka's representation of the facts seems to have been accepted by such later authorities as Hertwig (*loc. cit.*) and by Grosser(6) who (1909) copies Duval's schemata, or (1927) the schemes of Pytler and Strasser(8) which are evidently founded on Duval.

On the other hand Graf Spee(9), in his important monograph on the implantation of the ovum in the uterine wall in the Guinea-pig, has given expression to opinions entirely inconsistent with those of Selenka and Duval on this question. He emphatically rejects the view that there is present at any time in the implanted ovum of the Guinea-pig any such outer ectodermal wall of the blastocyst, transient or otherwise, as that represented by Selenka and Duval.

His explicit opinion to the contrary may here be quoted *literatim*: "Zu dieser Ansicht bin ich durch das Studium auch der späteren Stadien immer wieder zurückgekommen und betone dies hier nur deswegen, weil Selenka und nach ihm Duval von einer dem Ei zuzurechnenden vergänglichen Deckzellenschicht berichten, wie sie auch für das Ei der Ratte und Maus von diesen Autoren beschrieben wird, und die wie ein weiter Sack den grössten Theil des Eies einhüllen soll. Eine Deckzellenschicht dieser Art existirt beim Meerschweinchen ganz bestimmt nicht."

This decisive divergence from the widely accepted scheme of Selenka and Duval acquires special importance in view of the fact that this particular contribution of Graf Spee to knowledge of the early development and

implantation, *in utero*, of the ovum of the Guinea-pig has remarkably influenced subsequent embryological theory on the subject of mammalian implantation.

It is to me very surprising that several later writers (cf. Grosser, 1927), whilst professing to follow Selenka and Duval in their recognition of a transient ectodermal (trophoblast) wall of the blastocyst ("hinfälliges Ektoderm"), do nevertheless continue to accept without question Spee's version of the morphological characters of his early implantation stages. That interpretation carried with it for Graf Spee—as it was logically bound to do—the total repudiation of the existence of any wall or layer of "hinfälliges Ektoderm." The fundamental incompatibility of the two views of the constitution of the blastocyst will reappear in the further course of the argument of this paper.

Graf Spee's denial of the existence of even an evanescent outer trophoblastic layer in the implanted blastocyst has recently obtained energetic support from the findings of Dr Maclaren (*loc. cit.*).

It is the special object of the present communication to re-examine the grounds of the interpretation placed by Spee and Maclaren upon the constitution of the blastocyst of *Cavia* before, during, and immediately after implantation.

I hope to be able to show reason for the belief that that interpretation is in some material respects erroneous and retrograde and that Selenka and Duval were after all not mistaken in their recognition, in early implantation stages, of an ectodermal outer wall of the blastocyst, albeit of a somewhat exiguous and transient character.

Spee's analysis of the constitution of the Guinea-pig ovum prior to implantation is on the following lines: He refers to it as a blastocyst ("Keimblase"). Its cellular wall ("Keimhaut") is said to consist, in the equatorial region, of a single layer of flattened cells. Over that polar area characterised as "Implantationspol" (also as "Gegenpol"), it is likewise a single layer, but the cells are more cubical. Over the other polar area, facing the uterine lumen and designated "Placentalpol," he describes the cellular wall as showing a clump of cells ("Zellballen") projecting into the cavity. Clearly the ovum thus described corresponds exactly to the typical early blastocyst of other Eutheria, though the author omits any attempt at comparison with other types.

In other passages Spee refers to the blastocyst wall or "Keimhaut" indifferently as "äussere Zellhaut" and "äussere Eihaut." On p. 139 he affirms of the implantation pole of the "äussere Zellhaut" that it "bildet nach der Implantation die freie Eikuppe, in die die Embryonalkugel später hineinrückt und in der der Embryo sich ausbildet."

Now from an examination of his figs. 19 *PA* and 22 (cf. Plate I, fig. 8), it is perfectly evident that this "Eikuppe"—supposed by him to be identical with the implantation pole area of the early blastocyst—is none other than the cell layer which in its immediately subsequent history has obtained practically universal recognition as the "inverted" entoderm layer of the embryo.

It is true that I cannot find that Graf Spee himself does anywhere affirm or admit this identity but it is an inevitable consequence of the value he assigns to the layers of the implanted ovum of *Cavia*.

His position therefore involves the rejection—so far as the Guinea-pig is concerned—of that explanation of "inversion of the germ layers" which was furnished by Selenka. And it is to be associated, of course, with Spee's emphatic denial, already quoted, of the existence of a trophoblastic outer layer ("Deckzellenschicht") in any way corresponding to that described and figured by Selenka and Duval in the Rat and Mouse and by Selenka in the Guinea-pig also.

Maclaren has arrived at similar conclusions, on this matter, to those of Graf Spee and he has not hesitated to make explicit the opinion, which we have seen to be implied in the statements of the latter author, that the definitive "inverted" yolk-sac entoderm is actually the same cell layer as that which constitutes the so-called "implantation pole" area of the wall of the unimplanted blastocyst.

Both of these observers recognise and figure a blastocyst cavity as existing prior to implantation. Both of them hold that this cavity subsequently disappears during the process of implantation, either by collapse or by obliteration of the original cavity through increase of the "Zellballen" (inner cell mass) which is continuous with the "placental pole" of the early blastocyst. Thus for both of them the "ovum" during implantation is a solid morula with a central cellular core surrounded by an outer layer of cells. But whilst it would seem that Spee continues to regard the entire outer layer, including the "implantation pole" area or "Gegenpol" (his "Eikuppe"), as ectodermal, Maclaren, on the other hand, regards the latter area of the outer layer as certainly entodermal on account of its further destiny.

Now even apart from any question of homology, a reversion from the already attained condition of a normal Eutherian blastocyst to that of a solid morula would be an extraordinary phenomenon to manifest itself in the growing and developing ovum. It would be a retrograde change unparalleled in any other known Eutherian group, not excepting the closely related types of Rodents exhibiting "inversion" or "entypy." In the latter the blastocyst on implantation not only retains its cystic cavity but for a time this increases in extent, subject only to the compression and modification in form occasioned by the further intrusion into it of the amnio-embryonic primordium with its ectoplacental suspensorium. Only later does the cavity lose its character as its outer wall becomes more or less vestigial.

Is it really credible, then, that the ovum of the Guinea-pig should differ so fundamentally from even its nearest congeners?

The excellent figures of the pre-implantation blastocyst of *Cavia* which both Spee and Maclaren supply (Plate I, figs. 1 and 2) indicate the possession of a structural constitution which is indistinguishable in all its essentials from that of other Eutheria of corresponding stages. Indeed it is clear that, apart

from the question of the prospective significance of the various regions, no doubt could arise as to its identity with the latter. It exhibits a characteristic unilaminar "trophoblastic" wall with an inner "formative" cell mass ("embryoblast" of Rabl and Grosser) attached at one area of its interior.

Furthermore, the fact must not be ignored that Selenka (*loc. cit.*) has actually figured and described a series of successive stages of the blastocyst of *Cavia* in which he depicts in the most definite fashion the persistence, after implantation, of an outer trophoblastic wall, though in an obviously atrophying condition (Plate I, figs. 3–7).

In view of these positive records of Selenka I am unable to understand the statement of Maclaren (*loc. cit.* p. 117) that the presence of such a layer "has never been actually observed." It may be admitted that Selenka's figures are rather diagrammatic and I am ready to believe that he may have allowed himself some latitude in the direction of restoration or reconstruction. In themselves, therefore, they may not be admissible as conclusive evidence in regard to a disputed point. It should be remembered, however, that at that time the point was not in dispute and one is therefore entitled to regard his presentation of the case as at least more or less unbiassed. In any case, I find it hard to believe that what Selenka so very definitely delineates as an outer blastocyst wall in process of atrophic disappearance, in quite a number of different specimens (cf. Plate I, figs. 3–7), was wholly fanciful and merely the product of a vivid imagination.

I have myself made a careful study of serial sections of a number of early implanted blastocysts of *Cavia, in situ* in the uterine wall, from the Heape embryological collection in Cambridge.

Several of these are almost identical in stage with those illustrated in Spee's figs. 19 *PA* and 22 (Plate I, fig. 8), in which the ectoplacental suspensorium has begun to take form as a discoid thickening.

In these I have been able to recognise delicate cellular alar extensions from the marginal region of the ectoplacental disc. These alae taper off into single cells. They correspond to the "Seitenfalten" of Spee's fig. 22 (Pl. I, fig. 8) but they are very inappropriately described as folds. I am of opinion that Spee's explanation of their character is erroneous and I venture to suggest that they are actually vestiges of the proximal attachment of the evanescent trophoblastic outer layer, the "hinfälliges Ektoderm," auct.

In one of these specimens of Heape's I am confident of the persistence of definite remains of the parietal trophoblast layer itself.

However that may be, I submit that in view (*a*) of the comparative rarity of material for the study of critical stages; (*b*) of the technical difficulties in avoiding disturbance of delicate structural relations; and (*c*) the probability of considerable individual variation in the condition of a layer in course of absorptive disappearance; it will not do summarily to dismiss the evidence offered by Selenka as wholly unworthy of serious consideration.

I propose now to enquire more closely into the source of the discrepancy

between the accounts given respectively by Graf Spee and by Selenka. And I shall first claim as common ground—for reasons already given and in spite of Maclaren's opinion to the contrary—the admission of a complete homology between the different regions of the unimplanted blastocyst of *Cavia* and the very similar regions of the early blastocyst of other Eutheria.

In this connection I reproduce for comparison (Plate II, fig. 9) Duval's illustration of the early (unimplanted) blastocyst of the Mouse. Here the essential correspondence with Spee's and Maclaren's figures (Plate I, figs. 1 and 2) from *Cavia* is unmistakable, the only obvious difference being that in the case of the Mouse the differentiation of a definitive entoderm layer from the deep surface of the inner cell mass, or "embryoblast," has already taken place.

Plate II, fig. 10 shows a reproduction of Graf Spee's important fig. 7. In it the author illustrates one of the initial phases of implantation in the Guinea-pig. It is one of Spee's figures most commonly reproduced in text-books to illustrate the first step in "interstitial" implantation.

There is little difficulty in interpreting the condition of the ovum illustrated in this figure in terms of the normal Eutherian blastocyst, nor does the author himself introduce any discordant idea in his explanation of it. He still recognises the specimen as a "Keimblase" with a cystic cavity enclosed by the "Keimhaut" whose thin-walled implantation pole area has now become embedded, whilst the placental pole still protrudes into the uterine lumen.

It is in his reading of the structural features of his next succeeding stage (stage II) of the implanted blastocyst that Spee reveals his marked divergence from the views of previous observers.

The structural picture representative of the stage in question is shown by the author in several figures, one of which is here reproduced as Plate II, fig. 11.

It is deserving of notice that this stage was represented in Spee's series by one specimen only; and, further, that of this sole specimen only one thick section, containing three or four superimposed nuclear layers, remained intact and available for exact investigation.

It must be admitted that the figures he gives of this section yield only a rather confused picture of its intimate structure. The author himself admits some difficulty in deriving its structural arrangements from the condition of the previous stage ("Wenn sich nun auch wegen der erheblichen Dicke des vom Ei vorliegenden Durchschnitts und der nicht besonders scharfen histologischen Differenzirungen der Gewebstheile durch die dazu angewandte Pikrinschwefelsäure präcisere Angaben den obigen sich nicht zufügen lassen," etc.). Nevertheless he considers himself justified in drawing the fairly confident conclusion that the single layer of cells which at one side clothes the larger cell mass (Plate II, fig. 11) represents the earlier "Keimhaut mit Gegenpol"; whilst the cell mass itself represents the "Keimhügelregion" which has protruded into the former cavity of the blastocyst so as to gain contact with the "Gegenpol," thus completely filling up the cavity.

Incidentally Spee notes the fact that the total calibre of the ovum has not only not increased but even shows a trifling diminution as compared with the immediately previous stage. Elsewhere he remarks concerning this phenomenon "dass der Raum zwischen dem Zellballen und der hautähnlich dünnen ins Uterusgewebe vorgeschobenen Zelllage des Eies entweder durch Wachsthum des Zellballens ausgefüllt worden oder dass der Raum durch Collaps seiner Wand verschwunden sei."

I venture here to suggest that even of the unsatisfactory and inconclusive picture offered by Spee's figs. 8 and 8 *P* (cf. Plate II, fig. 11) an alternative explanation may be given. This is, that the original cavity of the blastocyst has not wholly disappeared but is still represented by the cleft-like spaces shown between the mass of cells and the supposed decidual zone surrounding it. Further, I suggest that the characters of the latter zone are attributable, not merely to a decidual reaction to the implanted ovum, but in part, at least, to the incorporation in it of material of the original trophoblastic "Gegenpol" of earlier stages. I suggest, indeed, that such an incorporation of atrophic trophoblastic material is already taking place even in the preceding stage shown in Plate II, fig. 10.

The next succeeding stages (III and IV) of Spee's series are separated only by the briefest intervals of time from his stage II, and from one another.

In Plate II, figs. 12 and 13 are reproduced two of his illustrations of his stage III, whilst in Plate II, fig. 14 there is shown a reproduction of his well-known fig. 11 representing his stage IV. The latter figure has found its way into most of the modern text-books and has there been accepted at its author's own valuation.

In all of these figures the apparent outer cell layer of the supposedly morular ovum now appears more definite and distinct. Where it covers the superficial surface of the mass and is still exposed to the uterine lumen it represents the "placental pole" and its significance as ectoplacental trophoblast is obvious and unquestionable. Its cells are specifically referred to by Spee (*loc. cit.* p. 174) as becoming the mother cells of the foetal placental tissue.

The question therefore arises: Is the remainder of this apparently continuous outer layer, where it covers the deep surface of the inner cell mass, to be regarded as of the same ectodermal (trophoblastic) nature as the superficial, placental pole, area with which it appears to be directly continuous? According to Spee, it is constituted by the original implantation polar area ("Gegenpol") of the "Keimhaut" or "äussere Eihaut." If so, its homology must certainly be with the thin trophoblastic wall of the ordinary Eutherian blastocyst.

On the other hand, there can be no doubt that, as Maclaren quite rightly insists, this same layer, which at this stage clothes the deep surface of the morula-like mass, is genetically identical with the layer of "inverted" entoderm of later stages. Maclaren nevertheless follows Graf Spee in identifying it with the thin implantation pole area of the wall of the unimplanted blastocyst.

In this latter identification I am convinced that both Spee and Maclaren are in error. The very definite layer covering the deep surface of the inner cell mass in Spee's stages III and IV, as well as later, has, I suggest, nothing to do with the thin wall of the early blastocyst but has itself been delaminated or differentiated as entoderm from the deep surface of the early inner cell mass itself. Its apparent continuity with the admittedly trophoblastic superficial covering of the inner cell mass is merely topographical and secondary, not genetic and primary. (Incidentally it may be noted that a comparison of Spee's figures suggests that the central core of cells of the inner cell mass appears to have undergone reduction during this suggested process of differentiation from it of an entodermal layer. But it would be rash to attach too much importance to this distinction.) I further suggest that on the evidence furnished by various illustrations of the structure of the unimplanted blastocyst of *Cavia* (Plate I, figs. 1 and 2) the question may well be raised whether the process of differentiation of entoderm may not already have begun prior to implantation, as appears to be the case in the Mouse (Plate II, fig. 9).

On the other hand, if Spee's interpretation of his stages III and IV be correct, it is well to recognise clearly what its acceptance implies. In the first place we shall have to recognise the occurrence of the extraordinary phenomenon of a sudden and complete obliteration of the already existing blastocyst cavity in a growing and developing ovum, i.e. its sudden reversion to the condition of a typical morula. In the second place we have to witness the strange and rapid transformation of the atrophic and exiguous distal wall of the blastocyst of Spee's fig. 7 (cf. Plate II, fig. 10) into a closely fitting layer of active, well-formed, cells which can easily be followed through all subsequent stages into the conspicuous columnar layer ensheathing the embryonic rudiment and as such universally recognised as inverted entoderm!

In opposition to this view I submit with some confidence the opinion that the phenomena exhibited by the blastocyst of *Cavia* during implantation are susceptible of an explanation less at variance with our knowledge of the characters of the early blastocyst in other "entypical" Rodents.

In order to bring out more clearly what I believe to be the true reading of Spee's and Maclaren's figures of the blastocyst of *Cavia* I reproduce herewith four figures of stages in the development of *Arvicola*, another member of the group of Rodents showing "inversion," as illustrated by Dr Sansom (10) in 1922.

The first of these (Plate III, fig. 15) may profitably be compared with Spee's figure of a very early blastocyst of *Cavia* (Plate I, fig. 1). In this latter figure I have suggested above that there is already some indication of commencing differentiation of the primordium of the entoderm from the "embryoblast" or formative inner cell mass, though I attach no great importance to this point. The *Arvicola* figure shows a somewhat flattened blastocyst towards the beginning of implantation. Here, at the so-called "placental pole" of Spee, we have a discoidal plate-like area of cubical trophoblast cells to

whose deep surface the inner cell mass is attached. The character of this trophoblast disc already foreshadows the ectoplacental suspensorium or "Träger." This is continuous marginally with the thin non-placental trophoblastic wall of the blastocyst which distally corresponds to the "implantation pole" area of Spee. As in the Guinea-pig, the cystic cavity is not very extensive and within it two small cell groups very probably represent entoderm beginning to be differentiated from the embryoblastic inner cell mass.

This structural conception is entirely borne out by the features of the next stage as seen in Plate III, fig. 16. On a merely casual glance at this figure one might be led to identify the now definite layer of entoderm with the thin trophoblast wall of the previous figure. To do so would be precisely to repeat what I believe to be the radical mistake of Graf Spee in the case of *Cavia*. A more attentive study of the figure will make it perfectly clear that the former trophoblast wall is still present although it now takes the form of a more or less syncytial layer closely applied to, and even partly incorporated with, the surrounding decidual zone.

The next succeeding stage in *Arvicola* (Plate IV, fig. 17) shows the entodermal layer now in the form of a completed vesicle, a condition which it never attains in the Guinea-pig. But the distal trophoblast wall—whilst preserving its marginal continuity with the ectoplacental disc—still persists as a somewhat mutilated, but nevertheless more or less continuous layer. And here I would direct special attention to the very definite preservation, in somewhat cuticular form, of the inner boundary of this now rather imperfect and more or less syncytial layer.

In a still later stage of *Arvicola* (Plate IV, fig. 18) the distal wall of the entodermal vesicle has now largely disappeared. Also the distal trophoblast wall has undergone further atrophy, probably through cytolytic change, almost to the point of disappearance. It is now little more than a thin syncytial or perhaps symplasmatic lining to the decidual encapsulating tissue. Nevertheless its inner cuticular-like boundary is still preserved, thus definitely limiting the original blastocyst cavity, whilst the original marginal connection with the now thickened ectoplacental disc is still maintained.

In the light of these illustrations of the constitution of the developing blastocyst of another "entypical" Rodent we may now return to the consideration of the condition in the Guinea-pig as seen in Graf Spee's series of figures. It is unnecessary to recapitulate the critical analysis of the figures already commented upon in previous pages. The alternative explanation of them already suggested is, I submit, elucidated and confirmed by the appearances presented by *Arvicola*.

Spee's celebrated fig. 11, however (Plate II, fig. 14), perhaps deserves some further remark on account of its general acceptance and reproduction in various treatises as exemplifying the alleged solid morular condition of the embedded ovum of *Cavia*. Thus in his recent work Grosser ((6), 1927) definitely accepts the morula-concept in the following terms: "Eine wohlausgebildete, vielzellige Morula, wie wir sie beim Kaninchen oder den Fledermäusen finden,

laszt nun (als weitere Verschiedenheit gegenüber niederen Vertebraten) einen deutlichen Unterschied zwischen einer oberflächlichen einreihigen Zellschicht und dem inneren Zellhaufen erkennen; die beiden Anteile entsprechen, wie die weitere Entwicklung lehrt, einerseits der Anlage des Chorionektoderms, anderseits der Anlage aller übrigen Teile, also vorzüglich des ganzen Embryos," etc.

On the other hand, Grosser does not follow Spee in entirely rejecting the idea of the temporary existence of a layer of "hinfälliges Ektoderm." In regard to this he would appear to follow the lead of Selenka and Duval; but he does not appear to have made any attempt to harmonise this view with the morula view of Spee. He does not betray any consciousness of their mutual incompatibility.

Accordingly he must be understood to believe (*a*) in agreement with Spee, that there is in the unimplanted blastocyst a thin trophoblastic wall; (*b*) also in agreement with Spee, that this wall becomes, on implantation, the outer layer of a solid morula; (*c*) in opposition to Spee, that somehow or other a thin and evanescent trophoblastic layer ("hinfälliges Ektoderm") comes to form the outer wall of the developing blastocyst. It is true, however, that although Grosser has not realised the incompatibility between the two views he espouses he is not completely satisfied with the position as it stands. This is evident from his remark ((6), 1909, p. 71), in reference to the constitution of the supposed implanted morula of Spee, "doch ist das Schicksal dieser Abschnitte noch nicht hinreichend verfolgt." Notwithstanding this he still, in 1927, accepts, in common with such other well-known authorities as Hertwig (*loc. cit.*), Bonnet (11) and Corning (12), the morula-like embryonic structure so prominent in Plate II, fig. 14 at the value attributed to it by Graf Spee. I again submit that the true reading of this figure is in terms of the process so clearly manifest in the series of figures of *Arvicola*.

When this figure is compared with Plate III, fig. 16, which repeats Sansom's text-fig. 2, the fundamental similarity of the two conditions is at once apparent. The only outstanding difference between them is that in *Arvicola* the antembryonic trophoblastic wall of the blastocyst has not yet wholly lost its identity—as later on it will—in the decidual surroundings.

In Plate V, fig. 19 is reproduced another of Spee's figures of a specimen which he classifies as belonging to the same stage IV. Although the author remarks that the figure does not afford an accurate understanding of the structural condition it is, in my opinion, deserving of attention. It appears to me that it falls perfectly in line with his important fig. 7 (Plate II, fig. 10) as exhibiting a slightly later phase. The conspicuous vacuolated spaces in Plate V, fig. 19 actually occupy the same relative position as the admitted blastocyst cavity in Plate II, fig. 10. The author however explains them quite differently—as liquefaction cavities in the midst of a symplasma resulting from histolytic change in the surrounding decidual tissue. On the lines of the process seen in *Arvicola* and indicated in Spee's own fig. 7 (Plate II, fig. 10, *mihi*) I suggest that the supposed liquefaction cavities really represent the

original small blastocyst cavity crossed by strands of coagulum. I further suggest that in the peripheral zone, marked "*l*" in the figure, there is to be recognised the site, and probably in part the vestiges, of the original thin "implantation pole" area of the blastocyst. I consider it beyond doubt that the cell layer now clothing the deep surface of the embryoblastic cell mass is entodermal in character and never at any time formed part of the original blastocyst wall.

In Plates V, VI, figs. 20–23 I herewith reproduce four other figures from Graf Spee's paper (his figs. 12 *P'*, 13 *A*, 17 *A* and 15). All of these figures show more or less similar features. All of them show the same morula-like mass, clad on its deep surface by a single layer of cells which is indubitably the future "inverted" entodermal layer. All of them show the solid cell mass as partly surrounded by a more or less crescentic clear space, Spee's "Saftraum"; Maclaren's "destruction space." All of them show this space to be limited peripherally by a sharp cuticular-like boundary—a condition very unlikely to result from a process of cytolytic destruction, where an irregular or ragged boundary would be much more likely. The decidual zone thus sharply limited irresistibly suggests the same explanation as the corresponding zone in *Arvicola*, of a syncytial or perhaps rather a symplasmatic compound of trophoblastic and decidual elements. In short, all the features exhibited by these figures of Graf Spee may best be explained on the lines laid down in the preceding pages.

The general conformity of Maclaren's figures of similar stages is unmistakable as will be evident from a comparison with Plate VI, figs. 24–5, which reproduce his figs. 2 and 3.

It is noteworthy that at the definitely later period corresponding to that of Spee's figs. 18–22 (Plate I, fig. 8); to Maclaren's fig. 5 and to similar specimens in the Heape collection; the cuticular boundary of the quondam blastocyst cavity breaks down more or less completely. But in the critical stages now specially under consideration the definite sharp boundary seems to be constant and the identity of the picture during this phase with Plate IV, fig. 18, after Sansom, is most striking.

Thus far no detailed reference has been made to the comparatively recent work of Pytler and Strasser(8) which deals with the development of *Cavia* subsequent to implantation. But inasmuch as the earliest stage personally investigated by these observers was one in which the amnio-embryonic primordial mass was already widely separated from the ectoplacental suspensorium their observations throw no light on the problem under discussion.

It may be noted, however, that in their résumé of the facts of earlier development they appear to follow Graf Spee closely in reference to the phenomena of implantation (apart from a probably inadvertent misapplication of Spee's term "Gegenpol"). In their conception of what may be called the post-implantation stage, on the other hand, they appear, like Grosser, to follow Duval. Their schematic figures, reproduced by Grosser in his latest work (*loc. cit.* 1927), are obviously founded on Duval's. They have not made

any attempt to determine how the post-implantation vesicular blastocyst of the Duval scheme is derived from the solid "morula" of Graf Spee.

In view of the foregoing critical review of the evidence furnished by Spee and Maclaren I suggest, with all respect to these observers, but with some degree of confidence, that the structural features of the early implanted blastocyst of *Cavia* ought to be interpreted not in the sense of their presentment, but rather along the lines which I have illustrated by means of Dr Sansom's figures of *Arvicola*.

It is evident that this interpretation will bring the process of development in the Guinea-pig once more into harmony with that of the other Rodents which exhibit the phenomena of "entypy" in their early development. In other words I contend that the morphological interpretation of the blastocyst of *Cavia* which was entertained by Selenka and Duval is fundamentally valid and correct and that Spee's later contribution—apart from the value it may still possess from the point of view of the *method* of implantation—has had the unfortunate result of introducing an unnecessary confusion into the current conception of the morphology of the blastocyst in this Rodent type.

In conclusion, I desire to reiterate that I make no claim in this paper to contribute new and original observations of the phenomena under consideration. My aim has been simply that of critical discussion and reinterpretation of facts and observations which are already on record in word and figure.

I am indebted to the Royal Society of Edinburgh for permission to reproduce figs. 2, 24 and 25 from Dr Maclean's paper on "Development of Cavia: Implantation," appearing in their *Transactions*, vol. LX, pt I, to the publishers of the *Zeitschrift für Morphologie und Anthropologie* for figs. 1, 8, 10–14 and 19–23, to C. W. Kreidel's *Verlag* for figs. 3–7, and to Librairie Félix Alcan for fig. 9 from Duval's *Le Placenta des Rongeurs*.

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## EXPLANATION OF PLATES

Fig. 1. Spee's fig. 6, blastocyst of *Cavia* of 6 days, 11 hours, with still intact zona pellucida and free in uterine cavity near a shallow epithelial fossa. It shows the typical characters of an early Eutherian blastocyst with unilaminar trophoblast wall and inner cell mass or "embryoblast" attached at one pole. It seems probable that the differentiation of the entoderm from the deep surface of the embryoblast has already begun.

Fig. 2. Maclaren's fig. 1, showing blastocyst of *Cavia* exhibiting essentially similar characters to those of fig. 1. Maclaren gives the age as 5 days. The blastocyst lies in a fossa or crypt of the uterine mucosa whose epithelium is yet intact.

Figs. 3–7. Reproductions of Selenka's figs. 3–7, representing blastocysts of the period from 6 to 7 days. In each of these a thin trophoblastic wall is figured, although it is relatively inconspicuous and in most cases evidently atrophic. In all except fig. 3 the separation between the embryoblast and the ectoplacental disc or "Träger" has already begun, whilst in fig. 6 the ectoplacental cavity is also indicated. The proximal or "visceral" layer of entoderm, clothing the deep surface of the embryoblast, is clearly differentiated. It has at these stages the appearance of being continuous with the ectoplacental trophoblastic disc. Genetically, however, it is certainly derived from the embryoblast which it covers (cf. fig. 9 of early stage of Mouse).

Fig. 8. Spee's photographic fig. 22, representing an implanted blastocyst of *Cavia* of 7 days. Here it is evident that the separation of the embryoblastic from the ectoplacental primordia is beginning. In accordance with his general view Spee regards the unicellular layer clothing the projecting embryonic mass as "äussere Eihaut"—the original implantation pole area of the blastocyst wall. According to the view enunciated in the present communication it is clearly entoderm. For further discussion of this figure see text, p. 356.

Fig. 9. Duval's fig. 79, early blastocyst of Mouse (two sections); the resemblance to the early blastocyst of *Cavia* (figs. 1 and 2) is obvious, though the differentiation of entoderm from the embryoblastic inner cell mass is here quite determinate.

Fig. 10. Spee's fig. 7, blastocyst of *Cavia* of 6 days, 10 hours, showing early phase of implantation process. The zona has disappeared. The inner cell mass is relatively large. The trophoblastic outer layer marked *a* is seen to extend deeply into, and around the periphery of the implantation fovea. The two small vacuoles shown at *v* lie in cytoplasmic material representing the original trophoblast wall. Spee himself refers to it as "das häutige Theil des Eies." The clear spaces *e* he regards (with justice) as the cavity of the ovum.

Fig. 11. Spee's fig. 8, representing his implantation-stage II. See discussion in text, pp. 351–2.

Fig. 12. Spee's fig. 9 *B*, representing his implantation-stage III. According to the author this figure illustrates the obliteration of the blastocyst cavity which was still present in the specimen shown in fig. 10 (*supra*). For him, the layer of cells now seen enclosing the central cell mass is the same layer which in fig. 10 lines the implantation fovea. The contention of the present paper is that the latter layer—already more or less atrophic in fig. 10—has now practically disappeared by incorporation in the decidual zone and that the well-marked layer covering the central mass on its deep aspect is the now well-differentiated entoderm.

Figs. 13–14. Spee's figs. 10 and 11; the author takes fig. 14 as the type of his implantation-stage IV, fig. 13 as belonging to the preceding stage. In all essentials they are, however, very similar. Fig. 14 has been frequently copied by other writers as illustrating the assumed morula stage of the implanted ovum of the Guinea-pig. The suggestion of the present paper is that the crescentic clear cavity surrounding the morula-like mass (Spee's "Saftraum") is in reality the representative of the original cavity of the blastocyst whose outer trophoblastic wall is still represented by vestigial material incorporated in the obviously much modified decidual zone around it. The cell layer clothing the central mass of cells towards the cavity is the entoderm.

Figs. 15–18. Sansom's text-figs. 1–4, illustrating the blastocyst of *Arvicola amphibius* during early stages of implantation. This series of figures is held to furnish the key to the correct interpretation of the constitution of the early implanted blastocyst of *Cavia*. In these figures the fate of the original trophoblast wall may be followed, up to the period of its merging, as a vestigial layer, with the decidual capsule. The entodermal relationships are worthy of special attention in their bearings upon the problem of the entoderm in *Cavia*.

Fig. 19. Spee's fig. 16, to be specially compared with fig. 10. See p. 355 of the text.

Figs. 20–23. Spee's figs. 12 *P'*, 13 *A*, 17 *A* and 15; the characteristics of these four figures are essentially similar. See p. 356 of text.

Figs. 24–25. Maclaren's figs. 2 and 3; these figures are obviously open to the same analysis, and demand the same explanation, as figs. 20–23. See p. 356 of text.

Fig. 4.

Fig. 2.

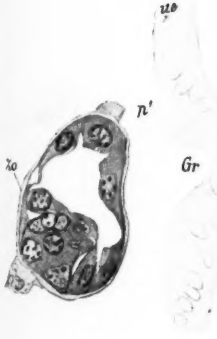
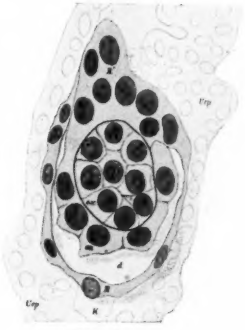



Fig. 1.



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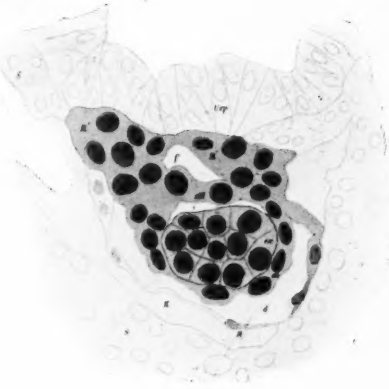

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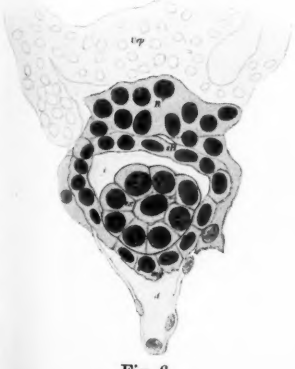

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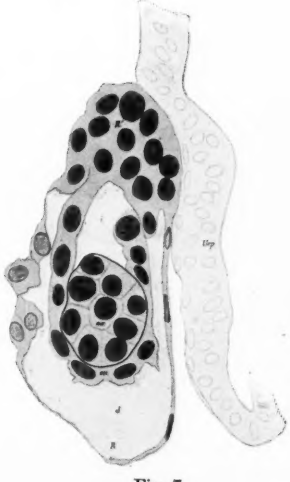

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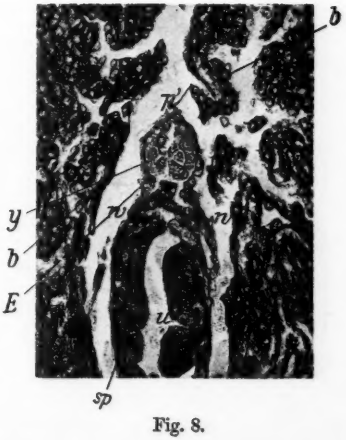


Fig. 8.

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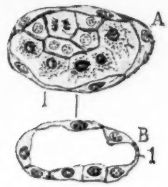


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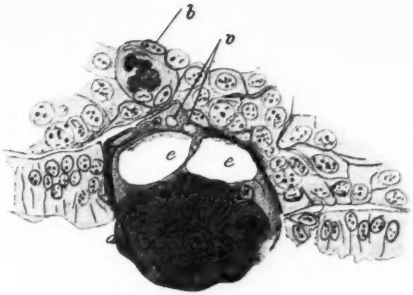


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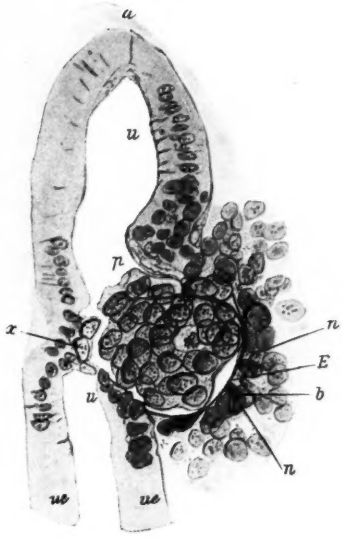


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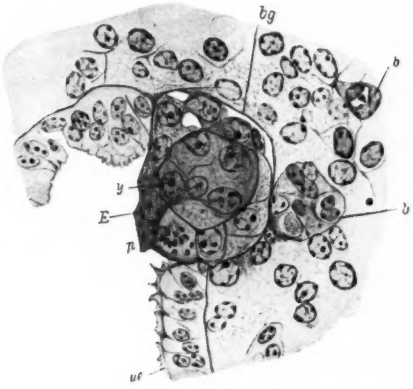


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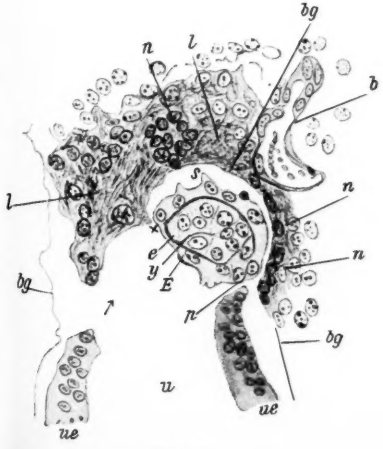


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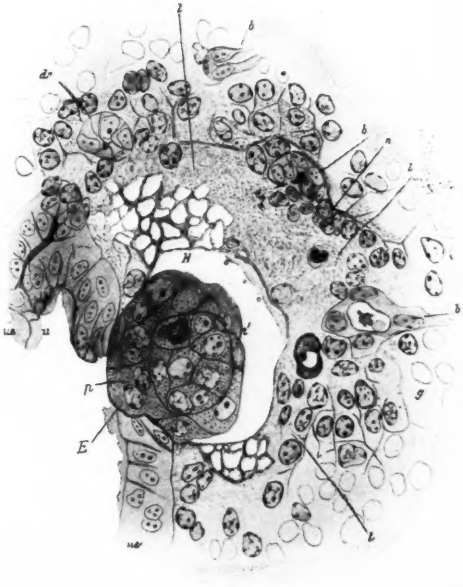


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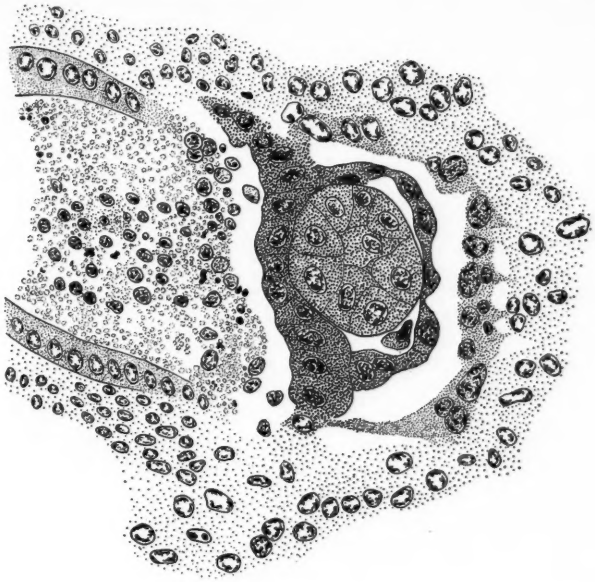

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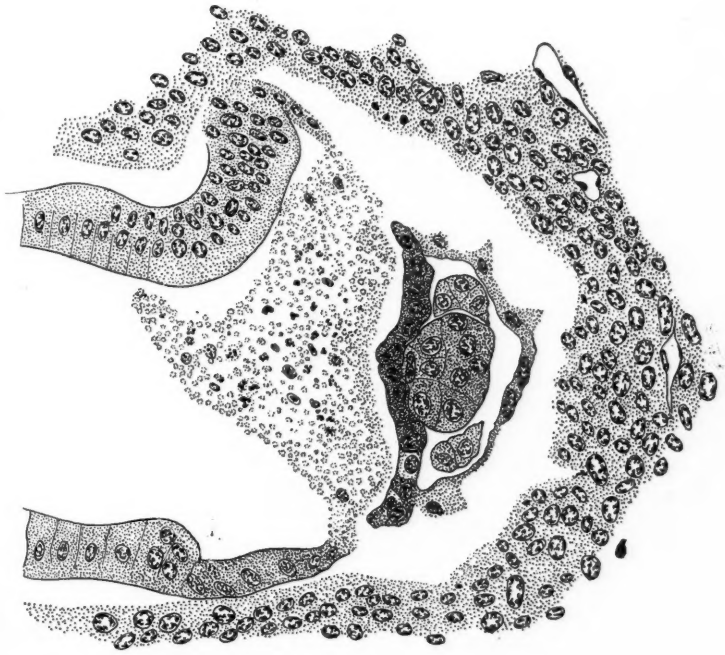

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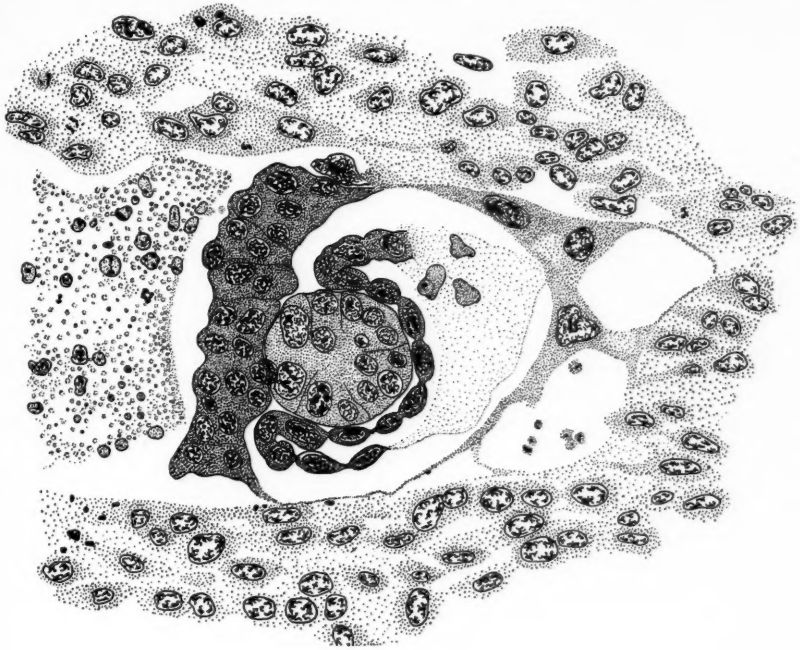

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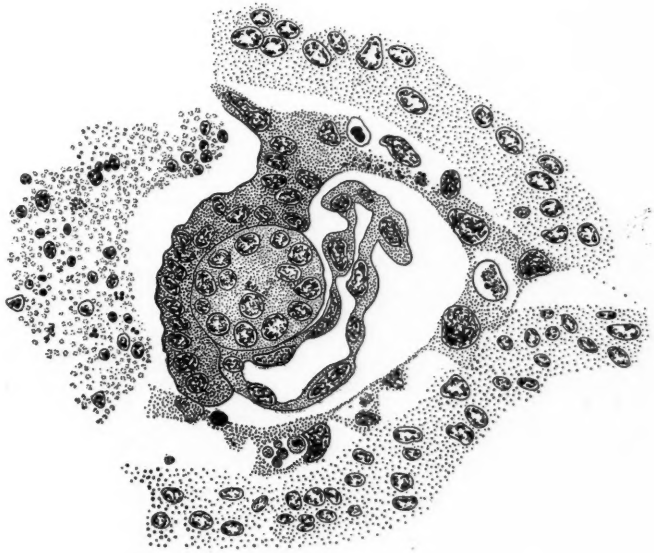

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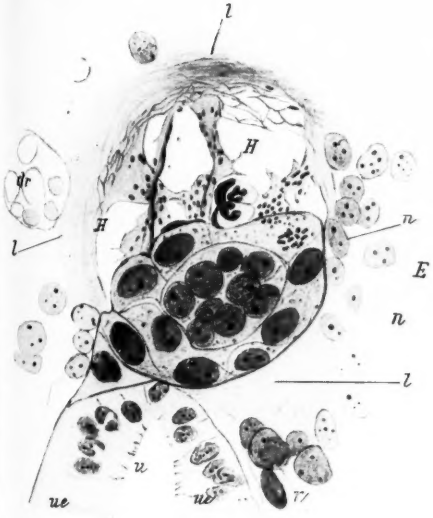


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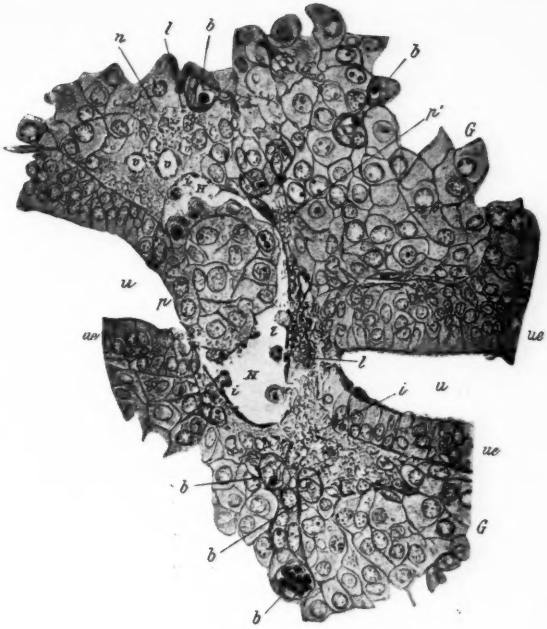


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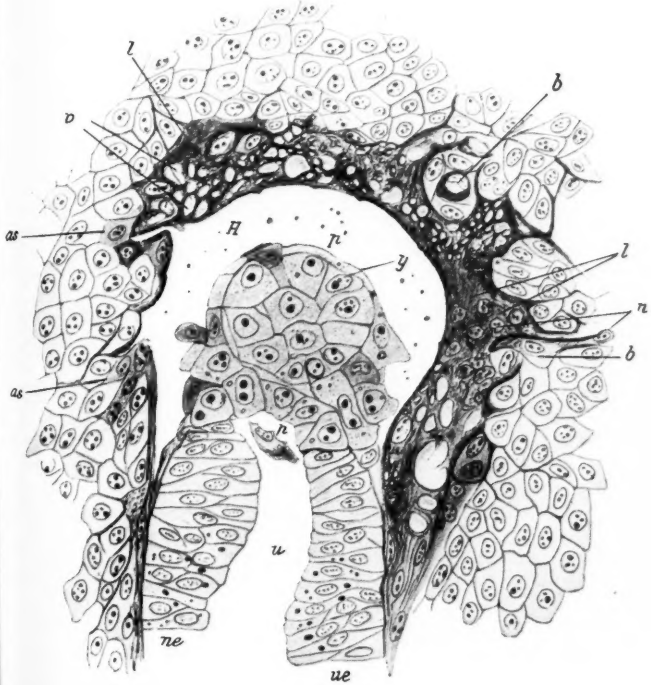


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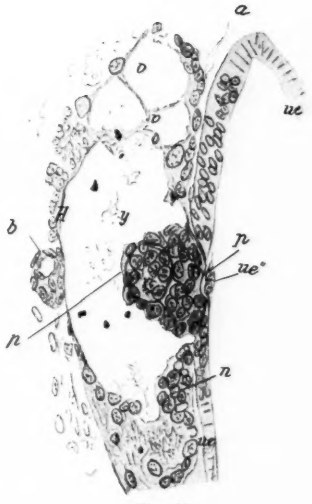


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Fig. 23.

Fig. 25.

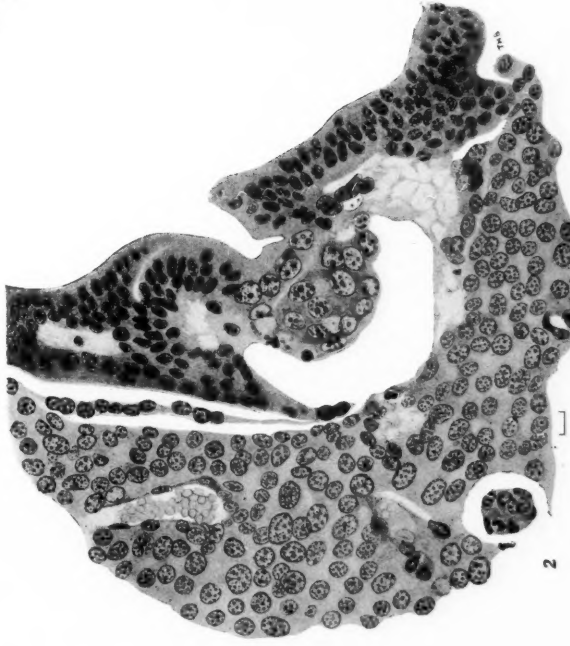


Fig. 24.

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# ANATOMICAL NOTES

## A NOTE ON THE SCALENUS MINIMUS MUSCLE

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THE inferior attachments of the scalenus minimus are not very fully described in the majority of the larger anatomical text-books, and during the course of an examination of the scalene muscles I was induced to make a careful investigation of the attachments of this interesting little muscle.

The conclusions at which I have arrived from this study are:

(i) The muscle is more frequently present, either as definite muscle tissue or fibrous remains, than is usually supposed.

(ii) Inferiorly it is inserted into the dome of the pleura and into the first rib. This decision is in agreement with the findings of Sebileau(1), who states that the pleural attachment is always present, while it disagrees with those of Bouchard(2), who considered the pleural insertion to be exceptional.

The mode of attachment to the pleura is in the form of a fan, usually more evident on the internal side of the insertion. The size of the insertion varies considerably, being sometimes as thick as $\frac{1}{4}$ inch, at other times so finely attached that it could be easily stripped from the pleura.

The attachment to the first rib is more interesting. The presence of the muscle always implies the separation from each other to a variable extent of the lower trunk of the brachial plexus and the subclavian artery, and we have here a means of solving the vexed question of the production of the markings on the upper surface of the first rib. In the photograph accompanying this paper of four first ribs, it is evident that the posterior part of the sulcus subclaviae is more markedly channelled than the anterior part, and it is significant to notice that in all four cases a scalenus minimus was present, which lends support to Wood Jones' theory.

The exact site of insertion to the first rib varies a little. It always has some attachment to the inner border of the rib, and in the majority of cases this is the only site. In a few cases it extends on to either the lower or upper surface. Occasionally the insertion is attached along the inner border, from the insertion of scalenus anticus anteriorly to that of scalenus medius posteriorly, or even extending a little further. In such cases there is little or no evidence of Sibson's fascia, and from our knowledge of the origin of Sibson's fascia this is what might be expected.

In the greatest number the inferior extremity of the muscle appears as a fine tendinous fasciculus gaining attachment to one small part of the inner border of the sulcus subclaviae, and if this is far enough situated from the

insertion of scalenus anticus, i.e. in the middle of the sulcus or thereabouts, there is almost invariably a small tubercle formed. When found on a macerated bone this tubercle serves as evidence for the previous existence of a scalenus minimus muscle. In the 50 bodies dissected in the course of this investigation, it was found that whenever this tubercle was present a scalenus minimus occurred. It is necessary to point out however that the absence of this tubercle on any bone does not exclude the presence of the muscle as it may fail to create an impression on the bone.

Wingate Todd (3), in an examination of 200 first ribs, found that the sulcus subclaviae was subdivided, either by a spicule of bone or by differences in bevelling, in 15 per cent. of them. In the study of 190 first ribs during this investigation, this accessory scalene tubercle was present in: 21 cases on the

Examples of first ribs with the accessory tubercle. *A.T.*=Accessory tubercle. *L.T.*=Lisfranc's tubercle.

right side (11 per cent.); 24 cases on the left side (12·6 per cent.); i.e. was present in 45 specimens out of 190 (23·6 per cent.). This number includes 60 from the Egyptian collection, which were probably damaged from the friction of sand, as all the muscle markings were slightly defaced, and they had a lower percentage than the modern ribs examined.

To complete the investigation the occurrence of the scalenus minimus was examined. This had previously been done by Zuckerkandl (4), and in the dissection of 60 bodies he had found it in: 22 cases present on both sides (44); 12 cases present on right side only; 9 cases present on left side only; i.e. was present in 65 out of a possible 120 (54 per cent.).

In the 50 bodies dissected for this paper it was in: 12 cases present on

both sides (24); 6 cases on right side only; 9 cases on left side only; i.e. was present in 39 out of a possible 100 (39 per cent.).

It is only natural that the muscle fails to leave a mark on the rib sometimes, when one examines the insertion of the much larger scalenus anticus. Frequently this impression is absent, and in one group of 20 ribs which were inspected Lisfranc's tubercle was only present on six. The size of the accessory tubercle bears no relation to that of scalenus minimus, and I am led to the opinion that its formation is passive, due to the pressure on the rib of the lowest nerve trunk of the brachial plexus, and the subclavian artery. In the first specimen illustrated there is a double groove occupying the sulcus subclaviae, suggesting that both structures take a part in the formation of the tubercle.

Where the muscle is present without the formation of a tubercle it would appear that there are two possible methods of insertion of the scalenus minimus:

(i) Where the insertion is along the whole of the inner border of the sulcus subclaviae, as previously noted. In these cases the inner edge of the sulcus is bevelled and often consists of a double border separated by a narrow groove in which a nutrient artery enters the substance of the rib.

(ii) Where the insertion is close to or incorporated with that of scalenus anticus. This is not uncommon, and when it occurs it is found that the subclavian artery is elevated from the upper surface of the rib, the sulcus being occupied by the lowest trunk of the brachial plexus.

In conclusion I should like to place on record my appreciation of much help given to me by Prof. J. S. B. Stopford, and by Dr A. J. E. Cave of the Anatomy department of Leeds University, in examination of ribs.

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# REVIEWS

*The B.N.A. arranged as an Outline of Regional and Systematic Anatomy.* By VICTOR E. EMMEL. (The Wistar Institute Press, Philadelphia.) 1927. Second edition. Pp. 256, with 12 plates. Price 3½ dollars.

The Basle Anatomical Nomenclature has been of great service in the simplification of anatomical terminology, for 50,000 terms have been reduced to 5000 by the removal of unnecessary synonyms. The opponents of the newer terminology are actuated by a love of the historical associations of some of the older names and by that natural conservatism which characterises the anatomist as distinct from the physiologist. The B.N.A. is essential to any worker who wishes to keep abreast of the additions to anatomical knowledge in other countries. This, it is true, does not protect the classical scholar in our midst from the shock of a large number of badly anglicised and debased latinisms. Practically all the recent anatomical publications in this country are written in the newer terminology because the American and Colonial Schools are warm adherents of the new vogue and so determine the market.

The inroads made on the time-table by the newer developments of Biochemistry and Physiology have reduced the time which can be devoted to dissection by the student. Yet, the Dissecting Manuals in use in this country have doubled in size as successive editions have appeared, thus making an unfair demand upon the time of the student and leading him into a maze of much reading at a time when he requires precise and purposive dissection in order to find his way about the body and imbibe those principles of Anatomy which are apt to be obscured by the very plenitude of detailed and uninteresting facts.

The teacher of Anatomy who is prepared to break away from tradition is now afforded an exemplary scheme for this purpose. Prof. Emmel insists on the students dissecting in unison, so that all are engaged on the same dissection with an adequate supply of cadavers to meet this demand. The first part of the book consists of all the terms met with in the routine dissection of the regions of the body. These terms are carefully arranged so that they give a summary of the part undergoing dissection. The plates indicate the bony points and landmarks, and the palpable and subcutaneous landmarks are in evidence. This part of the book resembles in a way the thumb margin of the old editions of Ellis's *Dissecting Manual.* The dissecting instructions are brief and concise, and the student is encouraged to study the structures by complete dissection. In this part of the book the anglicised forms of the B.N.A. terms are usually employed and the popular or personal name is frequently added. The extent to which some of the terms permit of ready and euphonious anglicisation has undoubtedly been one of the obstacles to the wider adoption of the newer terminology by the clinician.

The second part of the book consists of an arrangement of the B.N.A. terminology proper, without the English equivalents, in terms of the various systems of the body. An excellent system of cross references allows the student to find a particular structure under the regional and dissectional first part, or under the systematic second part. Those structures which are of ontogenic significance, such as the Venae umbilicales, are marked with an asterisk and those structures which are of slight practical importance, such as the individual muscles of the deep layers of the back, are indicated in a manner which helps to give the student a sound idea of the relative importance of structures.

This book is a valuable addition to the armamentorium of the teaching anatomist. The book, or a similar scheme, deserves to be tried in our schools. It calls for an adequate supply of cadavers and for a group of enthusiastic demonstrators. Those departments which are sufficiently fortunate to possess a good working museum and departmental library will thereby be enabled to give the student familiarity with the form and function of the human mechanism, and to stimulate that keenness for anatomical morphology which is in danger of disappearing under the present-day craze for treatises rather than hand-books of manual dissection. H. A. H.

*Einstellung zur Röntgenologie.* By Prof. Dr G. Holzknecht. (Wein: Julius Springer.) 1927. Pp. 115. Price 8.60 Reichsmark.

In his introduction Prof. Holzknecht recalls the fact that it is almost thirty years ago since he witnessed the introduction of Röntgen's discovery to the service of Medicine in Nothnagel's wards. The author has seen the upgrowth of modern Röntgenology and in this treatise outlines its future development. Only that short section wherein he touches on the means of investigating and teaching the anatomy of living subjects will prove of immediate interest to our readers.

*Clinical Researches in Acute Abdominal Disease.* By Zachary Cope, B.A., M.D., F.R.C.S. (Oxford: University Press.) 1927. 2nd ed. Pp. 214. Price 10*s.* 6*d.*

Although the title of this work is clinical it has an anatomical basis and deserves consideration by all who have to give a rational account of the anatomy of the abdomen. There is also a chapter on "Clinical Research" which will repay study.

# THE MUSCLES AND NERVES OF THE POST-AXIAL REGION OF THE TETRAPOD THIGH

## PART I

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## INTRODUCTION

WHILE the skeletal system has long occupied a prominent place in the comparative study of Tetrapoda, attention has been mainly directed to the study of features of direct classificatory value. The interpretation of bone form with consideration of the parts played by environment in ontogeny and phylogeny has been studied by comparatively few investigators.

Just as a study of bone form in ontogeny involves consideration of correlative differentiation (Roux) in relation to adjacent soft tissues such as musculature, so also in phylogeny the musculature requires consideration as an integral part of the immediate environment of bones.

The present investigation was undertaken for the purpose of tracing phylogenetic muscle changes among Tetrapoda, with a view to the subsequent examination of the relation in phylogeny between bone form and the muscular pattern.

It remains for subsequent work to extend the application of the criteria which have been developed for the determination of muscular changes in phylogeny. The main outlines alone of the structural evolution of the tetrapod thigh and pelvic region will be considered in this paper.

Attempts to reconstruct the soft parts and external form of the very numerous fossil Tetrapoda whose remains have come to light have given an impetus in recent years to the study of bones with reference to their relations with the soft tissues, especially with the muscles, in place of their study as isolated objects. In recent years, Watson, Gregory and Camp, von

Huene and Romer have essayed the detailed reconstruction of the musculature of various fossil groups. The principal difficulty, as Romer remarks, has consisted in the immature state of comparative myology.

Descriptions of the myology of many Tetrapoda, especially of mammals, are now available; but the diverse systems of nomenclature and the omission by many writers of all details regarding the course and distribution of nerves render the direct comparison of these forms by study of the literature both difficult and misleading. I have found that the attempt to infer the course of phylogenetic modifications of the muscular system through collation of existing accounts leads to many erroneous conclusions quite unjustified by the actual structural patterns of the animals concerned. The name "caudofemoralis" (and its variant "caudifemoralis"), for example, has been applied to at least three different mammalian muscles having distinct phylogenetic histories (*vide* Leche, Parsons, Forster and Carlsson, pp. 411 and 413), while the muscle to which Leche applied this name in menotyphlous Insectivora has in most descriptions of other mammals been either overlooked or described as pyriformis, quadratus femoris, or as some part of the semimembranosus or of the adductor musculature. Existing descriptions readily lend themselves to the support of views such as that of the former continuation of the biceps cruris as far as the caudal vertebrae, or that of the proximal migration of the insertions of the pyriformis and of the glutaeus maximus among mammals from more distal attachments to the middle of the femur and to the region of the knee respectively (*vide* pp. 424, 431). These views it has been found necessary to reject, as a result of re-examination of the animals on which they were based.

Of late there have been few substantial contributions to the myology of living Tetrapoda. The valuable study of the Salientia by Noble (1922) is important. Intensive studies of a restricted group like that of Noble on the frogs are indispensable alike for the tracing of adaptive changes within the group and for the morphological comparison of different groups. There can be no doubt that many of the mistaken homologies between reptilian and mammalian muscles, which have been suggested from time to time, are attributable largely to an inadequate knowledge of the mammals themselves (cf. p. 393, *infra*).

The conclusions I have reached are based on the dissection (aided in some instances by serial sections) of representatives of each class, and most of the recent orders of Tetrapoda, enumerated below. The data so obtained have been considered in conjunction with published figures and descriptions for the same or allied species.

At a meeting of the Anatomical Society (1923, p. 82) I drew attention to certain characteristic relations between the caudofemoralis (Leche) and the adjacent nerve trunks in Insectivora and other mammals. I further pointed out that the great retractor musculature of the hind-limb in reptiles and urodeles presents similar relations, and that these can be recognised also in

birds and frogs, despite the vestigial character of this musculature in them. In this paper it will be shown that the resemblance of structural pattern extends throughout the whole post-axial region of the thigh, and that it is much closer than a perusal of published descriptions would lead one to believe. Considerable apparent differences have proved to be illusory and the structural pattern has proved to be so similar throughout Tetrapoda as to leave little doubt regarding the general trend of muscle modification in the specialisation of the Salientia, Reptilia, Aves and Mammalia.

## The Homologisation of Muscles and Nerves.

The conception of homology rests upon the idea of a common descent of the organisms concerned ("homogeny," Lankester). The "identification" of a given nerve as a median nerve in various individuals (of the same or different species) is a method of structural classification, based upon the finding, after extensive comparative and variational studies, that the presence of a nerve with certain relations to adjacent muscles and bones is a conservative feature in limb structure.

Support is given to this mode of classifying nerves by the close relation which is found to hold between muscles and their nerve supply, provided only that the nerves are defined by means of their topographical relations in the limb.

The earlier attempts at the homologisation of muscles depended mainly on consideration of their relations to bones and to one another. Special value was attributed to a study of the site of "origin" (generally understood for this purpose to mean the more proximal attachment), as being more conservative in phylogeny than the distal attachment. The realisation of the close relation existing between muscles and their nerve supplies provided a valuable accession to the means of determining homologies, obscured as these sometimes are by the great changes of size and attachment which are involved in adaptive modifications of limbs and other parts. This really implied, however, the introduction of another parallel but independent conception—that of the homologisation of the nerves themselves.

This latter question has thus far remained in a generally unsatisfactory position. It is now desired to lay stress upon the importance of an adequate consideration of this factor.

Inasmuch as the "identification" of nerves is in common usage based, quite correctly, on topographical relations and not on central origin, the observed close relation of muscle and nerve supply implies a conservatism of the structural pattern of the thigh as a whole, involving not only muscles and their nerves, but also their topographical relations to the main nerve trunks of the limb. Neglect to consider this general structural pattern has led to the overlooking of close resemblances. The large buttock muscle, for example, of Monotremata has been generally but erroneously regarded as a "glutaeus maximus," evidently on the ground of its general position and

extent, and in spite of peculiarities of nerve supply (cf. Frets, 1909, p. 94) and insertion. Its nerve was accordingly described as N. glutaeus inferior. It will, however, be shown that this muscle presents all essential features (apart from its great size) of the "caudal slips of the hamstrings" present in many mammals and is still more like a reptilian muscle mass which has commonly been misinterpreted (*vide* p. 420, *infra*). An extreme instance of the conservatism of appendicular structure, despite great differences in the central origin of peripheral nerves, is offered by von Ihering's well-known observations on the innervation of the pelvic fins of Teleostei. The segmental origin differs greatly according as these are in an abdominal or in a jugular position, but fin structure (including the course of nerves within it) appears to have undergone relatively little change.

I have on a previous occasion (1922) given a preliminary outline of a classification of the mammalian adductor muscles based on consideration of the course of the obturator nerve, and especially on the course of the nerve to the gracilis. Such topographical details constitute a part of the structural pattern of the thigh.

Certain well-known exceptions have been claimed in regard to the constancy of the innervation of muscles. There is little doubt that certain of these depend on unsatisfactory muscle comparisons. Others, on the other hand, suggest further examination of the "identification" of the nerve in question, while there are still others, such as the peculiar distribution of the femoral nerve among Monotremata (Ruge, Westling), and the innervation of the interosseous muscles of the mammalian foot (Cunningham), whose significance cannot yet be estimated. But such instances are rare.

Comparative studies[1] may be said then to point to the topographical course of the principal limb nerves as an integral part of the structural pattern of the thigh, suggesting that their course and distribution depend on peripheral reaction systems during ontogeny rather than on the central origin of the nerves. What we know of the processes of nerve and limb morphogenesis may be claimed in support of this view. The well-known experiments of Roux and Braus with transplanted limb buds in Amphibia point to the course of a nerve bundle being an expression of its behaviour in a given environment, such as that offered by the limb bud to an outgrowing nerve. The general course and distribution of limb nerves are found to be the outcome mainly of developmental processes within the limb bud itself and not in the central nervous system. Przibram, in his summary of recent work relating to trans plantation and regeneration, finds that "a nervous influence on developing organs does not seem to enter into morphogenesis proper at all, neither in early development nor in regeneration" (1926, p. 324). If we restrict our

[1] It is appropriate to recall an instance of similar constancy in the course of a nerve-bundle, in the mammalian foot. Ruge and Cunningham (*Voyage of H.M.S. "Challenger," Zool.* vol. v, pt. xvi, p. 121) have shown that the lateral plantar nerve almost invariably passes between the adductor and flexor brevis series of intrinsic muscles, a feature which assists in their mutual distinction.

attention to the provisional motor elements of peripheral nerves (which originate primitively as collaterals from intraspinal tracts—Coghill, 1926, p. 117) it indeed appears that their formation may be initiated in the first place through the effects produced upon the embryonic spinal cord by the contraction of neighbouring muscle tissue (*vide* Kappers, 1921, pp. 143, 144). Their connection, moreover, with muscle is attained before there is perceptible nervous function (Coghill, 1926, p. 125). At a later stage it has been shown that the size of the spinal ganglia is in Urodela modified by alteration in the extent of peripheral musculature and integumentary areas (Detwiler, 1926, p. 411; cf. also Detwiler, 1924, p. 64). Detwiler's transplantations of larval Amblystoma limbs indicate, moreover, that there exists between the limb and its normal nerves an intimate developmental relationship (1922, p. 158). To these conclusions comparative anatomy makes its contribution by claiming a very close relation throughout phylogeny between peripheral muscles and the courses of nerves supplying them.

The foregoing considerations regarding the homologisation of nerves have had reference primarily to muscular nerves. The point of view upon which emphasis has here been laid clearly requires, however, that the conservatism or otherwise of the course of cutaneous nerves among limb structures should be examined from the comparative point of view. Some attempt has been made in the following pages to study this aspect of the structural pattern of the tetrapod thigh, in addition to the mutual relations of muscles and muscular nerves. For data regarding the course of cutaneous nerves I have been obliged to depend almost entirely on original observations.

Romer (1922, p. 522), in discussing the means at our disposal for the determination of the homologies of nerves, has denied that the course of a nerve in relation to adjacent muscles will prove its "identity," though he admits some constancy for the relations of nerves to bones. He instances Sieglbauer's observation regarding the variability of the course of the tibial nerve in Urodela in relation to the femorofibularis[1]. It may be added that other variations in the relations of nerves to muscles have come to light in the present investigation. But these do not invalidate the general conclusion that these relationships are extremely conservative in phylogeny. Sieglbauer's description of the nerve in question as a "tibial" nerve implies that its relations and distribution were sufficiently characteristic in every urodele examined to distinguish this nerve from neighbouring nerve trunks. It will be subsequently shown (p. 400) that the muscular relations of N. tibialis suffice to distinguish it throughout Tetrapoda from Nn. ischiadicus ventralis, peronaeus, and ischiadicus dorsalis. And when these nerves are thus identified by their topographical relations in the various tetrapod groups, it is found that the muscle-masses respectively innervated by these nerves present close resemblances in the various groups (those supplied by N. ischiadicus dorsalis and N. ischiadicus ventralis are reviewed in Part II

[1] Romer evidently intends to refer to this muscle, though he writes "femoro-tibialis" (*vide* Sieglbauer, 1904, p. 390).

of this paper). This circumstance is confirmatory of the value of the distinction provided by muscle relations. The variation in the course of N. tibialis cited by Romer is but an illustration of the classificatory character of nerve homologies, and does not invalidate our recognition of topographical relations, principally those with muscles, as the basis of the homologisation of limb nerves.

It is worthy of note, on the other hand, that the skeletal relations on which Romer rightly places some reliance, also exhibit minor variations comparable with those between muscles and nerves. In fish, for example, the pectoral girdle shows great variation in its relations to the appendicular nerves (Braus, 1898, p. 267), and this seems to find its most probable explanation, notably in *Polypterus*, in a phylogenetic remodelling of the girdle (Braus, 1900). The supracoracoid nerve also appears to have acquired a course in mammals differing from its passage through the procoracoid of therapsid and many other reptiles, presumably as a result of skeletal modification. Minor variations must be recognised in the relation of the median and radial nerves to the humerus among Tetrapoda, and their passage through foramina in some of them seems to be related to skeletal change. It may be that the absence in the hind-limb of frogs of a diazonal nerve is similarly related to change in the pubic part of the girdle, permitting the union of the obturator with the femoral nerve as Hoffmann (1878, p. 245) suggested, though Noble has offered an alternative explanation (1922, p. 53).

Romer's statement that de Man's attempt at homologising the finer nerves of Salientia and Urodela has proved valueless cannot be accepted *in toto*. De Man's comparisons, for example, between the nerves 11, 12 and 13 in the two orders (1873, pp. 56, 58 and 75) are sustained by Noble's comparisons (1922, p. 54) and find further support in the additional data presented in this paper. The exact point at which a nerve bundle leaves the main stem is, on the other hand, admittedly variable, as is also the precise arrangement of nerve branches to a muscle (Noble, 1922, pp. 50, 51).

Many instances have come to light in the present investigation of nerve bundles varying in their mode of union into larger trunks (identification being based on their course and confirmed by their distribution). Such variation is far more common than variation in the relations of nerve bundles to muscles or bones. Noble has offered an instance (1921, p. 50), in the union of the nerves to dorsal thigh muscles in *Pipa* and *Xenopus* into a common trunk, unlike other Salientia; but it appears that the relation to adjacent muscles, notably to the iliofibularis, was unchanged. The occasional "accessory obturator" nerve of man (better described—adapting Paterson's suggestion of 1891[1] to the B.N.A. —as the "accessory femoral" nerve) provides a similar instance. The thigh nerves subsequently to be described as Nn. ischiadicus dorsalis and ischiadicus ventralis (p. 372) will be shown to vary in the extent to which various constituent bundles are bound to one another and to the tibial and caudofemoral nerves. But despite these variations there is some constancy in the mode of union of nerve bundles. Those classified as elements of N. ischiadicus dorsalis in

[1] *Journ. Anat.* vol. xxvi, p. 47.

Tetrapoda are more closely associated with N. peronaeus than with N. tibialis in all cases studied. Similarly those classified as elements of N. ischiadicus ventralis are associated in the early part of their course with N. tibialis. Muscles presumed on other evidence to have had a recent phylogenetic differentiation from a common mass do in various instances pursue a common path until they approach their destination, as Noble (1922, pp. 26 and 51) showed for the "pectineus" and "adductor longus" of the frogs.

### On Muscle Homologies.

It is necessary to give further brief consideration to the meaning of homology in reference to musculature. The existence of intra-special *variations* in the muscular and nervous systems implies the classificatory character of our schemes of nomenclature. In the same way as the median nerves of various individuals can be grouped together, so the biceps muscles of the fore-limb can also be classified by the use of the name "biceps brachii." The term is applied even when one or two additional heads of origin are present, and from man is extended to the description of similar structures in apes and more remotely related animals. A limit is reached only when the necessary approximation of structure is wanting, and doubt exists as to which muscles should be considered "homologous" muscles. A hiatus in structural arrangement of this magnitude is not limited to groups supposed to have been delimited by the extinction of intermediate forms, but may occur as an intra-special variation, and anomalous muscles occur which cannot be closely compared with any normal ones.

No fundamental difference can be assumed to exist between "inter-specific" and "intra-specific" variation; such differences as there seem to be (e.g. Pearson, 1919, p. 373) may involve for the most part questions of interbreeding and its relation to geographical isolation or physiological isolation (e.g. through infertility). It is clear from experimental studies[1] that at certain developmental stages there are pluripotent tissues; a cell lineage in one individual might eventuate in the formation of muscle fibres, while in another it might result in the formation of areolar tissue. Thus we cannot yet say whether the musculature of an additional head to the biceps or of an anomalous abductor ossis metatarsi quinti in one man is represented in another by muscle tissue or by areolar or some other tissue. Slight genetic differences may lead to the formation of "anomalous" musculature by determining different histogenetic changes through altered metabolic or electrical gradients.

In the comparative study of muscles attention is focussed on their place in the developed organism as functional units in the mechanism of movement. Adaptive evolutionary changes are to be sought in modifications of attachments, internal structure or in changes of bone form which affect function. Muscles whose gross features show a definite evolutionary trend might well be found to show differences of cell lineage. But it is possible to trace the series of phyletic changes, even though the actual germinal differences

[1] *Vide* references provided by Przibram, 1926, p. 314.

and the epigenetic (or "apogenetic"—Przibram, 1926, p. 327) processes involved in muscle differentiation have not been analysed in detail.

It would seem essential for investigations of phylogenetic changes in a region such as the tetrapod thigh that comparisons should be made between the structures as a whole, *without* assuming too rigid an identity between the nerves of one animal and those of another, or a constancy of course and distribution of nerves throughout a phyletic series. Thus we may hope to trace phylogenetic changes, whether these consist in a change in course of a nerve bundle, in the relation between muscle cleavage and the zones of nerve distribution, in the attachments of muscles or in the courses of nerves supplying them. It is by means of such broad comparisons that the essential similarity of the thighs of Tetrapoda has come to light, obscured as it has been in published descriptions by the diverse terminologies employed; and it has proved possible to trace the main trends of phylogenetic modification in musculature.

## MATERIAL AND ACKNOWLEDGMENTS

In the animals enumerated below, the detailed distribution of nerves and topographical relations of nerves and muscles have been studied in the post-axial region of the thigh and adjacent parts of the trunk and shank. The conclusions reached are based mainly on the data obtained from these dissections. In addition, certain points have been checked in microscopic sections of embryos of *Alligator miss.* and *Chrysemys* sp. and of larvae of *Cryptobranchus allegh.*

Many of the mammals dissected belong to Dr Duckworth's collection, and my thanks are due to him for his kindness in so freely placing them at my disposal. I am greatly indebted to Dr Beattie for the opportunities he has provided me for the dissection of valuable material derived from the Gardens of the Zoological Society in London. I have pleasure in thanking Prof. J. P. Hill for a specimen of *Dasyurus mac.*, Prof. Sir A. Keith for a *Hyrax* sp., Dr Gadow for a *Crocodilus nil.*, and Mr Forster Cooper for his kindness in facilitating the study of material in the Museum of Zoology, Cambridge.

I take this opportunity of recording my great appreciation of the invaluable assistance I have derived from discussions of neuromuscular problems with Prof. J. T. Wilson, and my thanks for his permission to make extensive use of material in the School of Anatomy, Cambridge.

The following animals have been employed in the present study of thigh nerves and muscles.

**Mammalia.** *Ornithorhynchus anat.*, *Echidna acul.*
*Manis* sp., *Orycteropus cap.*, *Tatusia peba*, *Myrmecophaga jub.*
*Lepus cunic.*, *Mus dec.*, *Mus sylv.*, *Erethizon dors.*, *Dinomys branicki*, *Capromys melan.*, *Capromys brach.*, *Cynomys ludovic.*
*Macroscelides* sp., *Elephantulus myurus jamesoni*, *Tupaia pict.*, *Ptilocercus lowii borneanus*, *Erinaceus eur.*, *Talpa eur.*

**Mammalia** (continued). *Lemur lem., Lemur var., Lemur mac., Tarsius spectr., Loris grac., Nycticebus tard., Perodicticus potto, Galago crassic.*
*Pteropus med.*
*Hapale jacch., Hepales pigm., Chrysothrix sciur., Ateles ater, Ateles* sp., *Callicebus* sp., *Cebus* sp.
*Thepopithecus gel., Cynocephalus maim., Semnopithecus ent., Macacus rhesus, Nasalis larv.*
*Gorilla gor., Anthropithecus trogl., Simia sat., Hylobates leuc., Hylobates müll.*
*Lutra vulg., Meles tax., Paradoxurus herm., Mustela vison, Ursus himil., Felis cat., Canis vulg., Genetta vulg., Herpestes ichn.*
*Bos taur., Ovis ov., Sus scrofa.*
*Equus cab.*
*Hyrax cap.*
*Didelphys mur., Belideus sciur., Perameles obes., Dasyurus mac., Dendrolagus inustus, Sarcophilus harr.*

**Aves.** *Gallus bank. (var. Wyandotte), Columba liv.*

**Reptilia.** *Alligator miss., Crocodilus nil.*
*Varanus beng., Ctenosaura multisp., Uromastix spin., Lacerta vir., Gecko* sp., *Scincus* sp.
*Testudo* sp.

**Amphibia.** *Triton crist., Salamandra mac., Necturus mac., Cryptobranchus allegh.*
*Bufo vulg., Rana temp., Rana catesb.*

## A. THE STRUCTURAL PATTERN OF THE TETRAPOD THIGH (POST-AXIAL REGION)

### 1. Urodela. (Figs. 1, 2, 12 and 13.)

The topographical relations of nerve bundles to muscles are shown in fig. 1. Metazonal nerves enter the thigh as a single trunk, N. ischiadicus. Two of these, however, are in certain Urodela distinct from the remainder as they enter the thigh (e.g. *Salamandra mac.*, fig. 2); they will be described below as *Nn. pudendus* and *cutaneus femoris posterior*. At the proximal border of M. caudalifemoralis (de Man, 1873), the great retractor muscle of the thigh in primitive Tetrapoda, two nerves leave the main stem (which is continued to the leg as *N. tibialis*). These will be described as *Nn. fibularis* (Hoffmann, 1878) and *ischiadicus ventralis*.

N. ischiadicus ventralis[1] (comprising de Man's nerves 5, 6, 7, 8 and 9—1873) passes *ventrally* to the caudalifemoralis, and supplies the ventral thigh

[1] Frets (1909, p. 90) applied this term to a similar nerve (*vide* p. 396, *infra*) in *Sphenodon* and certain mammals; but he failed to recognise the corresponding amphibian nerve. Ogushi (1913) has applied the name of "N. pudendus" to a similar nerve in *Trionyx*.

muscles, named by de Man as follows: puboischiofemoralis externus (partim) and ischiofemoralis forming the deeper musculature (fig. 12); and pubotibialis, puboischiotibialis and ischioflexorius (forming the more superficial musculature). It includes also a cutaneous element which accompanies the nerve to the pubotibialis and becomes superficial on the inner side of the knee between

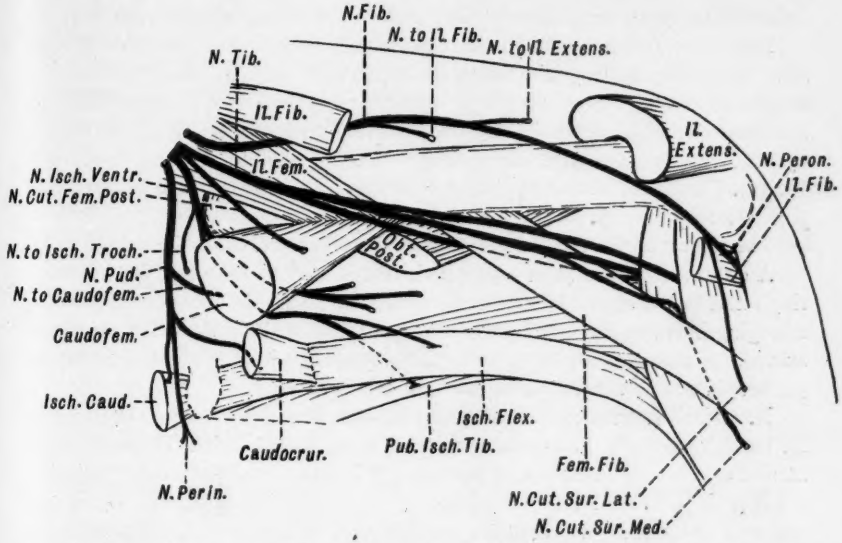


Fig. 1. Diagram of the post-axial region of the right thigh of *Cryptobranchus allegh.*, showing the topographical relations of nerve bundles to muscles. The structural pattern shown above is retained throughout Tetrapoda, apart from the presence here of two muscles, femorofibularis and the "caudocrural," which there is no reason to believe were present in the pro-amniota Amphibia. N. tibialis, distributed to the ventral part of the limb distal to the knee, passes between M. caudofemoralis[1] and M. iliofibularis. A small N. cut. fem. post. also emerges between these muscles. Nn. ischiadicus ventralis and pudendus, distributed to the ventral part of the thigh, and cloacal region, pass ventro-medially to M. caudofemoralis. The N. fibularis, distributed to the dorsal parts of the thigh, leg and foot, passes dorsally to M. iliofibularis from its pre-axial to its post-axial side, close to the knee. The relation of the tibial nerve (here shown as three trunks) to M. femorofibularis is variable among Urodela (cf. fig. 2).

Mm. pub.-tib. and pub.-isch.-tib. This cutaneous bundle will be named *N. cutaneus femoris ventralis*, in the belief that it corresponds with the nerve which will be so described in Salientia and Reptilia. In these classes, however, the nerve in question has a distribution mainly in the thigh, while the urodele nerve is mainly distributed in the shank.

[1] The names employed in the legends to illustrations are those which have been found appropriate for comparative tetrapod myology; their equivalents in the descriptions of various writers are provided on p. 434. M. caudofemoralis of the Urodela comprises M. caudalifemoralis (de Man) and perhaps also the caudo-crural of Humphry (*vide* p. 428).

N. pudendus, like N. ischiadicus ventralis, passes ventro-medially to M. caudalifemoralis, but is situated more caudally. It supplies this muscle, and also supplies three other caudo-appendicular muscles, viz. ileocaudalis[1], ischiocaudalis and caudalipuboischiotibialis (de Man)[1], the latter being the "caudo-crural" of Humphry (1872). Like N. ischiadicus ventralis, it includes a cutaneous element which will be named *N. perinaealis*. This nerve passes between the caudocrural and ischiocaudalis to reach the cloacal region.

The attachments and mutual relations of the above-mentioned muscles have been described by a number of writers[2]. It may be observed that the muscle described by de Man as a diploneural puboischiofemoralis externus is represented in some Urodela by two distinct muscles innervated respectively by Nn. obturatorius and ischiadicus ventralis (e.g. in *Salamandra mac.*, fig. 12). These will be distinguished as *M. obturator anterior* and *M. obturator posterior* respectively.

The remaining metazonal nerves pass *dorsally* to M. caudalifemoralis.

A cutaneous nerve (figs. 1 and 2) is distributed to the angle between the thigh and tail (a region it will be convenient to name the "*post-axial groin*"), emerging between M. ileofibularis[1] (de Man) and M. ischioflexorius (de Man). In view of comparisons to be made subsequently with mammalian anatomy (p. 399) it will be named N. cutaneus femoris posterior.

N. tibialis (figs. 1 and 2), like the N. cut. fem. post., passes dorsally to M. caudalifemoralis, but remains ventral to M. iliofibularis[1]. It divides into medial and lateral branches at the knee, if it has not already done so in the thigh (*vide* p. 375). Besides its branches to the muscles and skin of the calf and sole of the foot, it provides a small branch to the more distal part of the ventral thigh musculature (puboischiotibialis, cf. pp. 382, 399). Its cutaneous branch to the shank passes laterally to M. puboischiotibialis, a feature which distinguishes it from N. cut. fem. ventr. (*Necturus*—Appleton; *Siredon*—cf. Sieglbauer, 1904, p. 397). In view of its resemblance to the *N. cutaneus surae medialis* of mammals (p. 399), this cutaneous nerve will be given the same name.

N. fibularis differs from the above-mentioned nerves in regard to its relation to M. iliofibularis[1]. It is like N. tibialis and N. cut. fem. post. in its situation dorsal to M. caudalifemoralis, but (fig. 2) it passes between M. iliofibularis and the femur (clothed here by M. ileofemoralis[1]—de Man—and M. pectineus—Humphry), gains a superficial position by emerging between the iliofibularis and ilioextensorius of Sieglbauer (1904, p. 390) and Noble (1922, p. 47), and turns over the dorsal border of M. iliofibularis to reach the lateral (post-axial) surface of the fibula. It then disappears under cover of M. peroneus (Humphry)[3]. It innervates dorsal thigh muscles, Mm. iliofemoralis,

[1] The orthography employed by the various authors quoted has been respected. With this exception, the orthography employed in the text is that used in the table on pp. 434, 435, and in the legends to figures.

[2] Humphry (1872), de Man (1873), Hoffmann (1878), Sieglbauer (1904), and Noble (1922).

[3] M. femorofibularis—Hoffmann. 1878, p. 158. This name is, however, unsuitable since Humphry previously applied this name to another muscle (Mivart's "short head of biceps").

iliofibularis, and ilioextensorius, and enters the shank to provide muscular and cutaneous nerves for the dorsal parts of the leg and foot. It includes a cutaneous component which leaves the main stem as it winds over the dorsal surface of M. iliofibularis; it supplies the fibular side of the leg. In some urodeles a further cutaneous bundle leaves the main stem about the middle of the thigh and winds round the dorsal margin of M. iliofibularis (in *Salamandra mac.*). These bundles pursue so similar a course that they will be described together, as *N. cutaneus surae lateralis.*

It follows then that the large nerve bundles of the urodele thigh show differences in their relations to Mm. iliofibularis and caudalifemoralis. Nn. ischiadicus ventralis and pudendus pass ventro-medially to both (including the cutaneous components N. cut. fem. ventr. and N. perinaealis respectively). Nn. cutaneus femoris posterior, tibialis and cutaneus surae medialis pass dorsally to M. caudalifemoralis but remain ventral to M. iliofibularis, while N. fibularis (with its cutaneous component, N. cutaneus surae lateralis) passes dorsally to M. iliofibularis as well as M. caudalifemoralis. The cutaneous nerves subsequently pursue distinctive routes to the surface. N. perinaealis passes between two caudo-appendicular muscles, and N. cut. fem. ventr. between two of the long flexor muscles; N. cut. sur. lat. passes between two of the dorsal muscles (Mm. iliofibularis and ilioextensorius), while Nn. cut. fem. post. and cut. sur. med. pass between the flexor and the dorsal musculatures.

Differences occur among Urodela (even within a single species) in the distance over which nerve bundles are bound up together. The nerve to M. iliofemoralis may leave the main sciatic nerve independently of N. fibularis, or it may accompany the latter a short distance. Published descriptions illustrate these variations. Similar differences in the branches of N. fibularis have been observed by Noble in Salientia (p. 377 *infra*). The tibial nerve may divide into its medial and lateral terminal branches in the middle or even in the proximal part of the thigh, instead of at the knee. This difference appears to be related to a variation in the course of the nerve relative to M. femorofibularis (Humphry). Humphry has noted this variability (1872, p. 53), the two hind-limbs of an individual *Cryptobranchus jap.* differing in this respect; but whereas in one limb Humphry found the two nerves again joining after encircling the muscle, I have found in a *Cryptobranchus allegh.* that the medial branch divided into two bundles which re-united more distally (cf. figs. 1 and 2). In *Salamandra mac.* the whole of the tibial nerve passes laterally (post-axially) to M. femorofibularis, splitting to encircle the sciatic artery.

It is to be observed that the division of the tibial nerve into two branches, which occurs in some urodeles in the popliteal space, is not comparable with the division of the mammalian or salientian division of the sciatic nerve into tibial and (common) peronaeal nerves. It will be shown that the latter is a constituent part of the urodele N. fibularis (fig. 9). Thus Humphry's names for the two branches of the tibial nerve in Urodela ("internal" and "external popliteal" nerves) have been found unsuitable.

Variation in the course of a nerve relative to a muscle has been noted by Sieglbauer (1904) in regard to N. fibularis and M. peroneus (Humphry).

M. femorofibularis (Humphry) was described by Mivart as the "short head of biceps." But in its relation to N. tibialis (fig. 2) it differs from the mammalian muscle of that name; the latter, moreover, is justifiably claimed by Parsons and Klaatsch as a neomorph in mammals (fig. 10; further evidence of this is offered on p. 403). The phylogeny of this urodele muscle has not been determined. In view however of the absence of this muscle in Reptilia (and apparently also in birds and mammals), and of the undoubted specialisations which distinguish the hind-limb of modern Urodela from that of the early Tetrapoda (p. 427), it is presumed that this muscle is a caenotelic feature of the Urodela. Functionally, it offers a parallel to the short head of biceps found among Primates and Xenarthra.

The muscular branch of N. tibialis to the distal part of the long flexor musculature was described by de Man as entering M. pubotibialis in *Triton crist.* But in *Salamandra mac.* and *Cryptobranchus allegh.* I have found it supplying M. pubi-ischio-tibialis; Hoffmann confirms in respect of the former animal (1878, p. 243); in both of them the branch arose from the medial terminal branch of N. tibialis. Both it and N. cut. sur. med. leave N. tibialis *after* encountering M. femorofibularis (Humphry).

Some essential relations in Urodela may be summarised by enumerating structures in their topographical order on the post-axial side, in passing from the dorsal to ventral aspect: M. iliofemoralis, M. ilioextensorius and its nerve; N. fibularis[1]; M. iliofibularis and nerve; Nn. cut. fem. posterior, tibialis and cut. sur. medialis[2]; M. caudalifemoralis and nerve; Nn. ischiadicus ventralis and perinaealis; M. flexor cruris and Mm. ischiofemoralis (de Man) and obturator posterior.

Variation in the structural pattern of the urodele thigh involves the relative size and extent of attachment of muscles, and the distance along which nerves are bound up together. Two muscles exhibit variations in their relations to the larger nerve bundles, viz. Mm. femorofibularis Humphry and peroneus Humphry, femorofibularis Hoffmann (p. 375, *supra*). The general pattern of thigh structure, so far as the relations of muscles and nerves and the distribution of the latter are concerned, is found to be very similar throughout Urodela, with exceptions of the kind recorded.

### 2. Salientia. (Anura, fig. 9.)

For purposes of comparison with the Urodela, the salientian terms employed will be those mainly of Gaupp (whom Noble has followed in his recent contribution, 1922); the data provided by these authors have been supplemented and controlled by dissection of *Bufo vulg.*, *Rana temp.* and *Rana catesb.*, and by the descriptions of Perrin (1892) and Nussbaum (1898). Corresponding to the specialisation and increased number of separate muscles (p. 427, *infra*), there is some modification in the disposition of nerve bundles, but the essential topographical relations are the same as in Urodela.

A single nerve trunk, N. ischiadicus, enters the limb caudad to the pelvis.

[1] Including N. cutaneus surae lateralis.

[2] No muscle like M. biceps cruris in mammals (cf. p. 399) is inserted in the region of the knee between the last two and the first of these nerves.

It gives off two nerves which pass ventrally to M. "pyriformis" (fig. 9), while the main stem passes dorsally to that muscle, just as in Urodela two nerves (N. isch. ventralis and N. pudendus) pass ventrally to M. caudalifemoralis but the main stem (Nn. fibularis and tibialis) dorsally to this muscle. The distribution of these nerves also shows them to be comparable with the urodele nerves. The one is comparable with N. pudendus, for it innervates M. "pyriformis" (and a caudalipuboischiotibialis also in *Ascaphus*, the only frog in which this muscle is retained—Noble, 1922, p. 52), and continues ventrally to M. "pyriformis" to end as a cutaneous nerve like *N. perinaealis*. To the last-named nerve the term "N. cutaneus femoris posterior" is often applied; but it is inappropriate since commonly applied among reptiles and mammals to another nerve, represented (in some Salientia, only, according to Nussbaum, 1898, p. 455) by a small twig passing between Mm. iliofibularis and "pyriformis," and arising from N. ischiadici close to the N. pudendus. This twig will therefore be now described as N. cutaneus femoris posterior (as in other Tetrapoda). In *Rana catesb.* I found this nerve to be of fair size, little smaller, indeed, than the N. perinaealis which passes from N. pudendus to the skin on the other side of M. "pyriformis" (subsequently shown to be comparable with M. caudofemoralis of other Tetrapoda, pp. 379, 409). The other nerve passing ventrally to M. "pyriformis," named "ramus profundus posterior" by Gaupp, has an extensive distribution to the enormous flexor mass (Mm. flexor cruris and flexor profundus, *mihi*, p. 414), and comprises, as in Urodela, a cutaneous element reaching the surface by passing through that mass, viz. between Mm. gracilis and sartorio-semitendinosus (Nussbaum, 1898, p. 548). To this cutaneous element the name N. cutaneus femoris medialis was applied by Gaupp, but is unsuited for comparative work, owing to its employment in mammals for a branch of N. femoralis. A similar nerve has already been termed *N. cutaneus femoris ventralis* in Urodela (p. 373), and this name will be now given to it also in the frogs.

The urodele N. fibularis is represented by two nerve trunks, e.g. in *Pipa* and *Xenopus* (Noble), which both pass dorsally to M. "pyriformis," and round the pre-axial side of M. iliofibularis, supplying the muscles on the dorsal aspects of thigh and shank respectively; these will be distinguished as *N. ischiadicus dorsalis* and *N. peronaeus* respectively. The arrangement differs from that described in Urodela (fig. 9) in the early separation of nerve bundles destined for the dorsum of the thigh from those for the dorsum of the shank, and the close apposition of the latter, as a distinct peronaeal nerve, to N. tibialis in the thigh. In most Salientia the disintegration of the N. fibularis has proceeded further and N. ischiadicus dorsalis itself is represented by bundles leaving N. peronaeus at different points for M. iliofemoralis, M. iliofibularis, and M. glutaeus with cruralis. The cutaneous bundle N. cutaneus surae lateralis remains associated with N. peronaeus as far as the knee; it was described by Gaupp and Nussbaum as "ramus cruris lateralis" of N. peronaeus.

The N. ischiadicus dorsalis is figured by Nussbaum (1898, figs. 2 and 3)

as passing between the "long" and "short" heads of "biceps"; these two muscles evidently are Gaupp's Mm. iliofibularis and iliofemoralis. The passage between them of the nerve to the dorsal post-axial thigh musculature is characteristically like the course of nerve bundles destined for that musculature

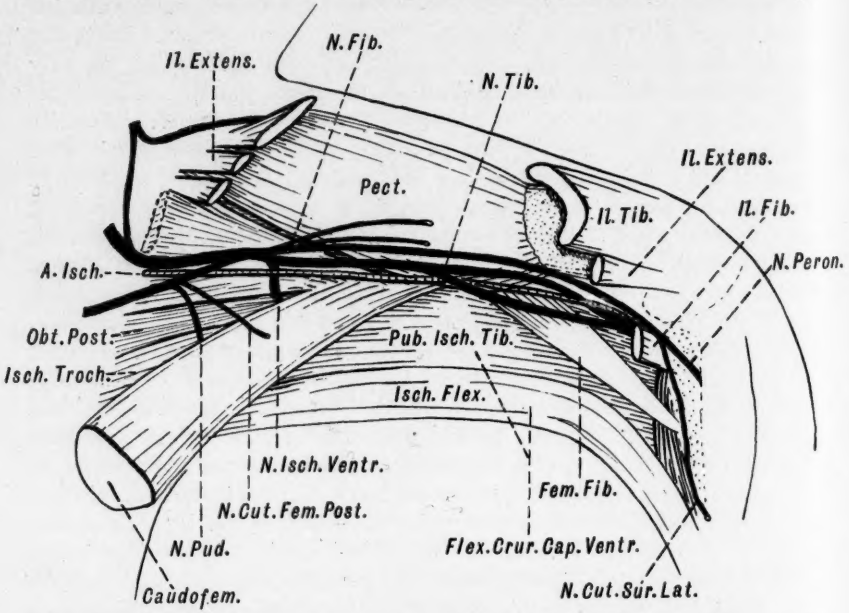


Fig. 2. Dorsal view of *Salamandra mac.*, with the right thigh in a position of medial (pre-axial) rotation, × 5. Parts of Mm. iliofibularis, ilioextensorius and iliotibialis have been removed. Two nerves, pudendus and ischiadicus ventralis, pass ventro-medially to M. caudofemoralis. The remaining trunks, Nn. tibialis and fibularis and the small N. cutaneus femoris posterior, all pass dorsally to that muscle. Of these N. fibularis passes round the pre-axial side of M. iliofibularis and over its dorsal margin to reach the leg. As it lies between M. iliofibularis and the Mm. iliofemoralis and pectineus it provides branches for dorsal thigh muscles; these branches are represented by N. ischiadicus dorsalis of other Tetrapoda (cf. figs. 3 and 9) and the continuation of the nerve, the N. fibularis, by their N. peronaeus. The figure shows the passage of N. tibialis laterally to the characteristic urodele M. femorofibularis, and its encircling of A. ischiadica; these relations are variable in Urodela (cf. fig. 1). It is to be observed that the whole of the musculature innervated through N. ischiadicus ventralis (long flexor muscles) passes to its pelvic attachment on the ventral aspect of M. caudofemoralis (cf. fig. 3).

in Urodela, between Mm. iliofibularis and iliofemoralis (de Man). It will be shown subsequently that the mammalian name of "biceps" is as misleading when applied to these muscles as is Gaupp's name of "pyriformis" for the salientian muscle now shown to exhibit all essential features of the urodele M. caudalifemoralis (de Man).

N. tibialis is closely associated, as already mentioned, with N. peronaeus

in the thigh, and thus passes between Mm. iliofibularis and "pyriformis" just as in Urodela it passes between Mm. iliofibularis and caudalifemoralis. I find no record of a branch leaving this nerve after passing dorsally to M. "pyriformis" for the supply of the distal part of any hamstring muscle (M. flexor cruris), comparable with the distal nerve supply recorded in Urodela (and in reptiles and mammals, p. 399).

The post-axial thigh nerves of Salientia are thus found to agree closely in course and distribution with those of Urodela, provided that Nussbaum's "long head of biceps" be admitted as the representative in frogs of M. iliofibularis and Gaupp's "pyriformis" as the vestige of the once large caudalifemoral musculature. These identifications have already been inferred by Noble (1922, pp. 52–54) on other grounds. According to Nussbaum (1898), the "pyriformis," now identified with the urodele caudalifemoralis, is absent in some of the Salientia.

### 3. Reptilia. (Figs. 3, 12, 13 and 14.)

Gadow's descriptions have been supplemented and controlled by dissections of various Chelonia, Crocodilia and Lacertilia (p. 416), and by the accounts of *Sphenodon* published by Osawa and Frets, and of *Trionyx* by Ogushi. Subsequently to my dissection of *Alligator miss.* Romer published (1923) an account of its limb myology in which he reached the same conclusions as myself with regard to Gadow's M. pubi-ischio-femoralis internus Theil I + II, M. pubi-ischio-femoralis post. Hauptheil, and M. iliofibularis II. These are recognised as parts of M. obturator posterior and M. adductor (Gadow would call them M. pubo-ischio-femoralis externus and M. ischiofemoralis), and M. extensor iliotibialis, respectively.

As in Salientia, N. peronaeus is closely associated with N. tibialis till near the knee (fig. 9). A N. ischiadicus dorsalis is recognised, comprising two nerve bundles which leave the tibial-peronaeal stem independently (cf. figs. 1 and 2). The more proximal of these supplies M. iliofemoralis, the more distal one Mm. extensor iliotibialis (Gadow) and iliofibularis (Gadow); but in the Lacertilia, M. iliofemoralis receives no supply from this source, and (except in Monitors) M. extensor iliotibialis receives none (Gadow, 1882, p. 380).

Gadow's "Hautast d. N. peroneus profundus" (1882, pp. 352 and 354) is found in the alligator to be a cutaneous nerve, passing dorsally (fig. 3) to the insertion of M. iliofibularis near the knee; it is therefore now renamed *N. cutaneus surae lateralis*, like the similar nerve of Amphibia. This nerve has also been recognised in *Lacerta vir.* and *Varanus beng.* Nn. peronaeus and ischiadicus dorsalis pursue in reptiles the same course[1] relative to M. femorocaudalis (Frets, 1909)[2], as that relative to M. pyriformis (Ecker, Gaupp and

[1] Gadow has shown certain of these relations in his figs. 34 and 37 (1882). His "iliofibularis I" of the alligator alone corresponds to the amphibian iliofibularis. His "iliofibularis II" presents all the features of a posterior differentiated portion of M. extensor iliotibialis or of a urodele M. ilioextensorius; it presents a similar relation to N. peronaeus (cf. figs. 2 and 3).

[2] *Vide* Table on p. 434.

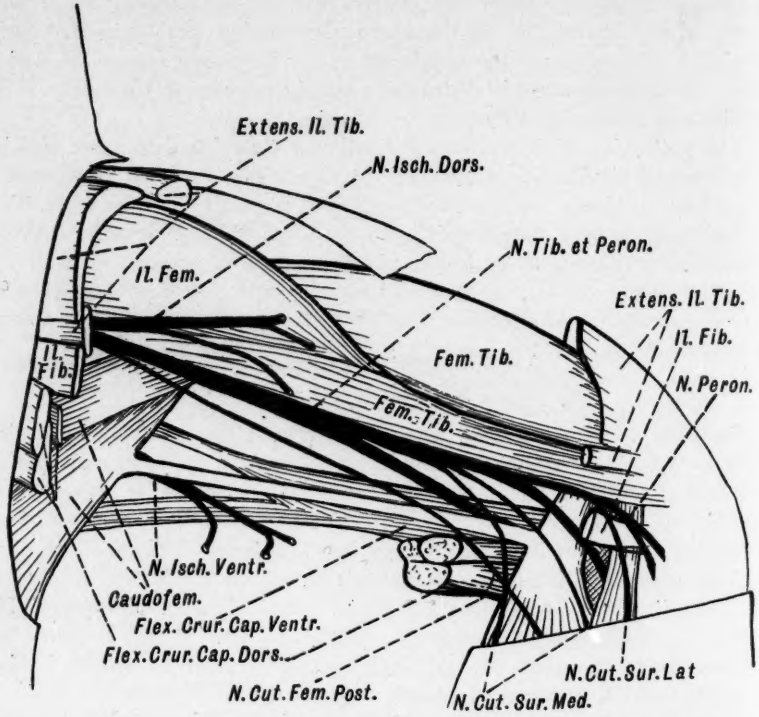


Fig. 3. Dorsal view of *Alligator miss.* × 1½, with the right thigh in a position of medial rotation, for comparison with fig. 2. As in that figure, the origins and insertions of Mm. extensor iliotibialis and iliofibularis are represented as cut short. In addition, the dorsal head of M. flexor cruris, which is wanting in Amphibia (figs. 1, 2 and 13), is represented as cut away in part, to show the course of N. ischiadicus ventralis ventrally to M. caudofemoralis. This nerve innervates the dorsal as well as the ventral head of M. flexor cruris, the nerves of supply being represented cut short as they pass dorsally on the distal side of M. caudofemoralis. The small ventral head of M. flexor cruris is provided with three heads of origin, the third of which is shown in fig. 12.

N. fibularis of Urodela is represented by two large nerve trunks, N. ischiadicus dorsalis and peronaeus, which, like the fibular nerve, pass round the pre-axial side of M. iliofibularis to their destinations; thus there has here been a segregation of muscular nerves destined for the dorsal part of the thigh from those destined for the leg and foot. A similar change has occurred in other Amniota and in Salientia (fig. 9). A N. cutaneus surae lateralis similar to that of Amphibia is again present.

N. cutaneus femoris posterior is unlike the corresponding nerves of Urodela and Salientia in its large size and distal extension beyond the knee; in this respect Reptilia resemble other Amniota. N. cutaneus surae medialis of Amphibia is represented in the alligator by two nerves.

Noble) in Salientia; the course is the same also as that relative to M. caudali-femoralis in Urodela (figs. 1, 2, 3, 9 and 14).

A N. ischiadicus ventralis leaves the main tibial-peronaeal stem and passes ventro-medially to M. femorocaudalis (Frets, 1909), a muscle to which the general tetrapod term of "caudofemoralis" will be found applicable (p. 409). This nerve forms a single trunk supplying superficial and deep ventral musculature in the post-axial region. It also supplies the dorsal head of M. flexor cruris (which comprises parts of the muscles described by Gadow as Mm. flexores tibialis internus and externus). The course of the nerve bundles to this dorsal head is like that of the bundles supplying the ventral head, as far as the distal margin of M. femorocaudalis; then they turn dorsally with a somewhat recurrent course (which is most pronounced in Lacertilia owing to the extension of the dorsal head into the tail, fig. 14). Gadow has recorded the innervation of the more dorsally attached flexor or "hamstring"[1] musculature from a nerve leaving the plexus independently, though pursuing a similar course to the nerve supply of the ventrally attached flexor musculature. I have not met with this condition. In the alligator and crocodile, in *Lacerta vir.*, *Uromastix spin.* and *Varanus beng.*, the nerve supply of the dorsal head of M. flexor cruris was closely associated with that of the ventral head on the ventral aspect of M. femorocaudalis, forming a single trunk, which I have named N. ischiadicus ventralis. It is inferred that the dorsal head of M. flexor cruris is a part of the same muscle as the ventral head, and that it has been formed by extension dorsally of a urodele-like M. flexor cruris, over the lateral surface of M. femorocaudalis (a conclusion which is considered further, on p. 416). The distribution of N. isch. ventr. to deep muscles is stated on p. 414. The cutaneous element of N. ischiadicus ventralis described in Amphibia (N. cut. femoris ventralis) is represented in Reptilia. It is identified as the nerve which pierces M. pubi-ischio-tibialis (in the alligator this muscle was described by Gadow as a part of "flexor tibialis internus"; that it is probably a part of M. pubi-ischio-tibialis was recognised by Gadow himself, 1882, p. 404, footnote).

N. pudendus of Amphibia is represented in reptiles by several distinct bundles arising directly from the plexus. There is a nerve supplying part of M. femorocaudalis (Frets)—Gadow's "caudi-ilio-femoralis," and several other nerves for the main mass of that muscle in Crocodilia and Lacertilia. A cutaneous element, mentioned by Gadow in the Crocodilia, and present also in Lacertilia as I have ascertained (*Lacerta vir.*), passes ventro-medially to M. femorocaudalis and emerges *between* the dorsal and ventral heads of

[1] The superficial ventral thigh musculature of reptiles is diploneural, as in mammals; the term "hamstring" or "M. flexor cruris" (p. 414) is reserved for that part which receives a metazonal innervation, though it is recognised that in various reptiles (mostly Lacertilians), in Monotremata, and rarely in Urodela, there is no plane of cleavage in the superficial ventral muscle mass corresponding to the boundary between the spheres of innervation of Nn. ischiadicus ventralis and obturatorius (*vide* p. 422, and the descriptions of Gadow, Westling and Noble).

M. flexor cruris. It is thus like that described in Amphibia as N. perinaealis; a similar nerve will be shown to exist in mammals.

Nerves to pelvi-caudal muscles also arise independently from the plexus (Gadow, 1882, pp. 362 *et seq.*); thus the pudendal nerve trunk described in Amphibia appears to be represented by a series of independent nerve bundles.

N. tibialis passes distally along the thigh dorsally to M. femorocaudalis just as in Amphibia it passes dorsally to M. caudalifemoralis (or the Salientian representative, p. 379), but it leaves the peronaeal nerve when the latter passes round to the dorsal aspect of M. iliofibularis, again resembling Amphibia. Its constituent bundles are subdivided near the knee by the long tendon of M. caudofemoralis (which is in most reptiles thus provided with a more distal insertion in addition to that on the femoral shaft). Cutaneous elements are distributed to the lateral aspects of thigh and shank after passing between Mm. femorocaudalis and iliofibularis. The most proximal of these, a long nerve, thus corresponds to the Amphibian N. cut. femoris posterior (figs. 3 and 9). Two other nerves pursue a similar course, but accompany the tibial nerve till nearing the knee; they are derived from Gadow's "Stamm III" and agree in their course and distribution with N. cut. surae medialis of the Urodela (the more distal of these appears to be that described by Gadow, 1882, p. 352).

The nerve which, in Urodela, supplies the distal part of M. flexor cruris after passing with N. tibialis dorsally to M. caudalifemoralis, is represented in the Crocodilia by the branch described by Gadow as leaving his "Stamm III" for the supply of M. flexor tibialis (1882, p. 353).

The post-axial thigh nerves of Reptilia thus present an arrangement closely resembling that of Amphibia; in the close association of N. peronaeus with N. tibialis in the thigh they are more like Salientia than Urodela. The additional nerve supplying M. flexor cruris caput dorsale (which is absent in Amphibia), accompanies N. ischiadicus ventralis as far as the distal margin of the great retractor of the thigh, M. femorocaudalis (Frets). M. femorocaudalis presents attachments and nerve relations like those of the urodele M. caudalifemoralis.

### 4. Aves.

A single N. ischiadicus enters the limb, and the nerves for dorsal thigh muscles separate early from those for the dorsum of the shank, as in frogs and reptiles; N. peronaeus proceeds with N. tibialis till close to the knee. A N. ischiadicus dorsalis is recognised, as in reptiles, arising in two stems from the main N. ischiadicus, the one for supply of Mm. glutaeus medius and glutaeus externus, the other for Mm. "tensor vaginae" and "biceps" (Selenka, 1869, and de Man, 1873, p. 98).

The cutaneous element already described for Amphibia and reptiles as N. cut. surae lateralis is represented again by a similar nerve leaving N. peronaeus near the knee, after passing with that nerve dorsally to the insertion of M. iliofibularis (cf. de Man's Plate II and p. 98, nerve No. XXIV).

In the fowl and pigeon I have verified the passage of Nn. peronaeus and ischiadicus dorsalis dorsally to M. caud-ilio-femoralis Gadow ("adductor longus"—de Man), and then round the pre-axial side of M. iliofibularis ("biceps"—de Man). These relations are like those relative to Mm. femorocaudalis and iliofibularis in reptiles, to Mm. "pyriformis" and iliofibularis in frogs, and to Mm. caudalifemoralis and iliofibularis in urodeles.

A nerve identified as N. ischiadicus ventralis supplies muscles named caud-ilio-flexorius and ischio-flexorius by Gadow (1891, pp. 162 and 166); it passes ventrally to Gadow's caud-ilio-femoralis, just as in other classes it has been seen to pass ventral to the caudofemoral musculature. These muscles correspond to the caput dorsale and caput ventrale respectively of M. flexor cruris in reptiles (pp. 381, 419). N. perinaealis (*vide infra*) passes between them.

The proximally situated M. ischiofemoralis Gadow ("quadratus femoris"—de Man) is innervated through an independent branch of the main sciatic stem, but its close resemblance to the reptilian M. ischiotrochantericus and to the urodele ischiofemoralis (de Man) points to this nerve being a segregated portion of the primitive N. ischiadicus ventralis. Gadow has described a cutaneous element (1891, p. 420) passing ventrally to M. caud-ilio-femoralis to reach the perinaeal region; its course and distribution identify it as N. perinaealis of other classes. Another cutaneous nerve mentioned by this author as reaching the shank after close association with the nerves to his muscles 36 and 37 (p. 420) appears to be the N. cut. femoris posterior; he clearly figures this nerve (e.g. Taf. XXIII *a*, fig. 1) passing dorsally to M. caud-ilio-flexorius and caud-ilio-femoralis, but ventrally to M. iliofibularis, and I have found it in the fowl and pigeon. It appears to be the nerve XVII of de Man (1873, p. 98).

The distal innervation for M. flexor cruris already mentioned for the alligator and various urodeles is closely reproduced by the nerve supplying the "accessory" insertion of caud-ilio-flexorius (Gadow, 1891, p. 421 and Taf. XXIII *c*); the nerve bundles have in each instance passed with N. tibialis dorsally to the caudofemoral musculature. Gadow (1891, p. 422) has mentioned a cutaneous branch of N. tibialis which appears to correspond to the N. cut. surae medialis of other classes.

The principal features of neuro-muscular topography are clearly shown in Gadow's Taf. XXIII *b*, figs. 2 and 4, and Taf. XXIII *a*, where the passage of Nn. peronaeus and ischiadicus dorsalis dorsally to Mm. iliofibularis and caud-ilio-femoralis, the passage between these muscles of Nn. tibialis and cut. femoris posterior, and the passage ventrally to both of them of N. ischiadicus ventralis, are seen to offer a close resemblance to reptilian conditions. M. caud-ilio-femoralis presents relations like those of the reptilian M. femorocaudalis (with which it is identified), and Mm. caud-ilio-flexorius and ischio-flexorius are respectively identified (p. 426 *infra*) as the dorsal and ventral heads of M. flexor cruris. The innervation of M. caud-il. fem. has, with reduction in size and a situation mainly in the thigh, become closely associated with N. ischiadicus ventralis (cf. mammals). N. pudendus has disintegrated

with separation of perinaeal components from the motor nerve for M. caudi-ilio-femoralis.

### 5. Mammalia. (Figs. 4–12, 14 and 15.)

The structural pattern of the thigh of the more primitive Mammalia has been misinterpreted in various respects, mainly owing to attempts to describe it in terms of the structures found in the more specialised mammals. The confusion may be attributed to our earlier and more exact acquaintance with a number of these mammals, among which may be cited man and various domestic animals.

An investigation of the thigh structure of some of the more primitive mammals has revealed a structure sufficiently like that in surviving reptiles (and birds) to justify the detailed comparisons which will be here attempted. The conclusion is reached that the structural pattern of the tetrapod thigh has become obscured in the more specialised mammals mainly by the loss of certain muscles[1], but also by the reduction in size or change of attachment of muscles; further, great extension and differentiation of certain muscles[2] has complicated the picture in other directions.

The most satisfactory account of thigh structure among the less specialised mammals is that provided by Leche for the Insectivora. He not only recognised Mm. caudofemoralis and femorococcygeus as distinct entities in mammalian myology, but he correctly recognised some of the resemblances between the thighs of Monotremata, Reptilia and Insectivora. His account will therefore be taken as a basis for the terminology and for a discussion of mammalian conditions. In regard to the Insectivora, it has been found that certain amendments of Leche's descriptions are necessary; and considerable additions have been required in regard to the course of cutaneous nerves.

#### (*a*) *Revision of the Insectivora.* (Figs. 4, 5 and 6.)

**Menotyphla.** Examples of *Tupaia pict.*[3] and *Macroscelides* sp.[3] have been dissected. It is worthy of note that Leche's descriptions[4] bring out several points of difference between these animals. Mm. femorococcygeus and glutaeus maximus are not at their origin distinct from one another in *Tupaia*; both arise from the vertebral column. In *Macroscelides*, M. femorococcygeus has a distinct origin from the tuber ischii, but, as in *Tupaia*, it overlies N. ischiadicus. To Leche's account we may add that *Tupaia* resembles *Macroscelides* in the presence of a separate insertion for M. femorococcygeus on capsular

[1] Caudofemoralis; tenuissimus; flexor cruris caput dorsale.

[2] Iliofemoralis; ischiotrochantericus; flexor cruris caput ventrale.

[3] By the kindness of Prof. Le Gros Clark I have recently had the opportunity of dissecting specimens of *Ptilocercus lowii born.* and *Elephantulus myurus jamesoni*. The features under discussion in this paper are similar in *Ptilocercus* and *Tupaia*, and in *Elephantulus* and *Macroscelides* respectively.

[4] Supplemented by Carlsson's descriptions (1909 and 1922) of various other Tupaiidae and Macroscelididae.

structures of the knee joint, while the glutaeus maximus is attached mainly to the third trochanter.

Leche observed that a M. caudofemoralis in *Tupaia*, with a caudal origin, is closely reproduced in *Macroscelides* by a muscle taking origin, not from the vertebral column, but from the tuber ischii. The characteristic relation to

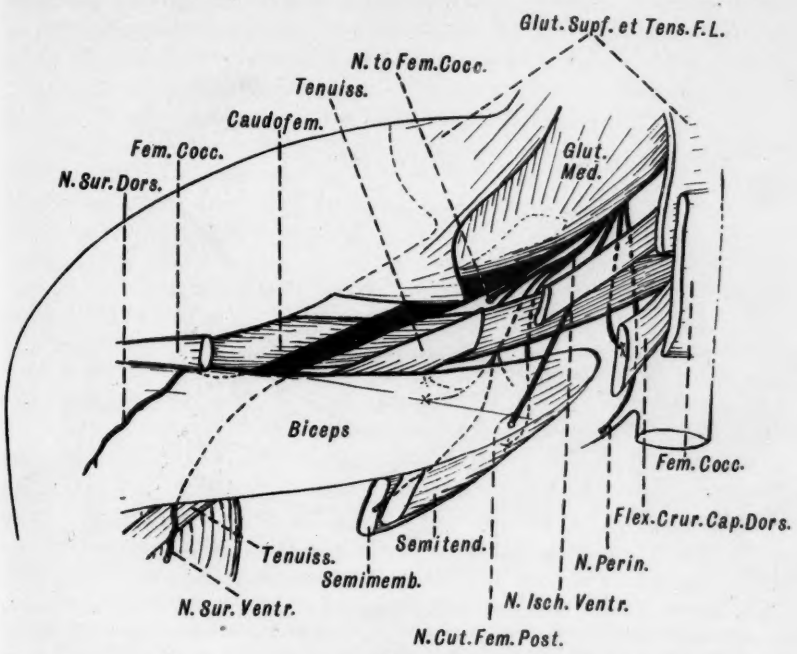


Fig. 4. *Tupaia pict.* ×2¼, illustrating most of the features of a primitive eutherian thigh (cf. figs. 5–14). Dorsal view, with the left thigh in a position of medial rotation; for comparison with fig. 3. Parts of Mm. glutaeus superficialis and femorococcygeus, of the dorsal head of M. flexor cruris, of Mm. semimembranosus and semitendinosus have been cut away, as also a short piece of M. iliofibularis (tenuissimus).

As in reptiles, M. flexor cruris comprises a dorsal as well as a ventral head, but the former is small and the latter large. Both are supplied by N. ischiadicus ventralis, which as in all Tetrapoda passes ventrally to M. caudofemoralis; the nerve to the dorsal head here pursues a somewhat independent course from N. ischiadicus. The ventral head of M. flexor cruris of mammals has acquired an attachment on the lateral side of the leg (M. biceps) besides its medial attachment (Mm. semimembranosus and semitendinosus); N. cutaneus surae lateralis is represented by two nerves, N. surae dorsalis and N. surae ventralis, passing respectively dorsal and ventral to M. biceps. As in reptiles, N. perinaealis passes ventrally to M. caudofemoralis (figs. 1 and 14) and between the two heads of M. flexor cruris; and M. cutaneus femoris posterior passes between Mm. iliofibularis and caudofemoralis. Nn. tibialis and peronaeus pass dorsally to M. caudofemoralis as in other Tetrapoda, the latter dorsally also to M. iliofibularis (fig. 9). A specialised feature of *Tupaia* consists in the differentiation of M. femorococcygeus from the glutaeal musculature. Its nerve, a component of N. ischiadicus dorsalis, passes dorsally to M. iliofibularis, like the latter nerve in other Tetrapoda.

N. ischiadicus (to which it is medial as it approaches the femur) and the relations to adjacent muscles are similar; the two muscles were homologised. He also observed that tenuissimus and the caudal head of semitendinosus, found in *Tupaia*, are unrepresented in *Macroscelides*. The latter animal is thus characterised by the suppression of four caudal muscle attachments. The origins of two muscles (femorococcygeus and caudofemoralis) have been transferred to the tuber ischii, and two other muscles have disappeared.

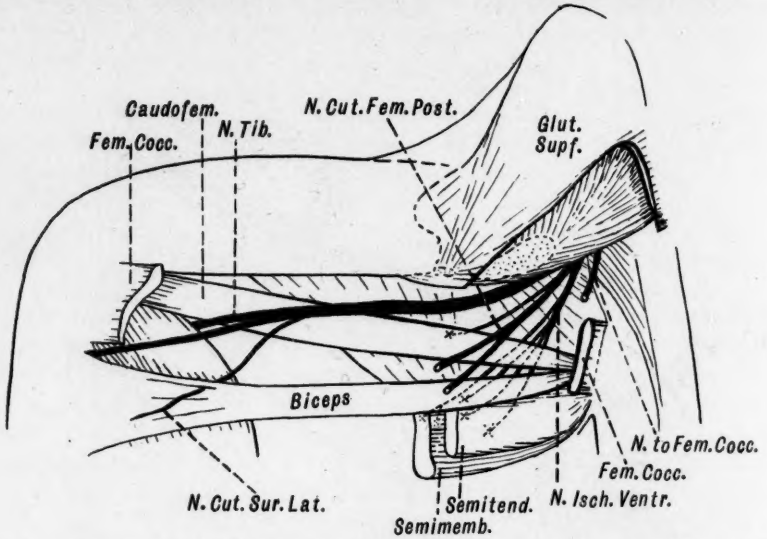


Fig. 5. *Macroscelides* sp. Left thigh, $\times 2\frac{1}{4}$, position and dissection similar to that of *Tupaia* in fig. 4. Modifications of the muscle arrangement seen in *Tupaia* consist in the loss of M. tenuissimus, and of the dorsal head of M. flexor cruris, and in the transference to the tuber ischii of the origins of Mm. femorococcygeus and caudofemoralis. Muscle-nerve relations are like those of *Tupaia*, excepting those involved in the above muscle changes; N. cutaneus femoris posterior, for example, is not separated from the nerve to femorococcygeus by a tenuissimus. The innervation of M. biceps from N. ischiadicus ventralis (and not as described by Leche) is illustrative of its derivation in phylogeny by differentiation of M. flexor cruris (cf. fig. 1). A single N. cutaneus surae lateralis is present (as in *Elephantulus*, p. 394).

Further examination of these animals serves to support and strengthen the inferences made from Leche's data. The resemblance of the two ischially attached muscles of *Macroscelides* with the Mm. caudofemoralis and femorococcygeus respectively of *Tupaia* is even closer than Leche realised.

*M. femorococcygeus* is in the Menotyphla superficially disposed between Mm. glutaeus maximus and biceps (figs. 4 and 5). Two cutaneous branches of the peronaeal nerve reach the surface on the lateral aspect of the knee[1]. Of these, one, the N. surae ventralis, passes in *Tupaia* (fig. 4) between tenuissimus and biceps, but in the Macroscelididae examined both tenuissimus

[1] This statement does not refer to the Macroscelididae.

and the N. surae ventralis are wanting. The other cutaneous branch, N. surae dorsalis, has a different course, for it passes between biceps and femorococcygeus (or pierces the margin of biceps), in all four members of the Menotyphla which have been examined (cf. footnote, p. 394).

The nerve to femorococcygeus passes dorsally (superficially) to the muscle identified as "caudofemoralis"; it thus differs from the course of the nerves to the hamstring muscles and of the nerve to the biceps in particular. The latter distinction fails in Leche's account owing to his erroneous account of the innervation of biceps (*vide infra*, p. 388). M. femorococcygeus is dorsal to both Nn. peronaeus and tibialis (like the glutaeal musculature).

Differences in the relations of this muscle in *Tupaia* and *Macroscelides*[1] depend mainly on its enormous size in *Macroscelides* and on special features in adjacent muscles, viz. (1) the loss of tenuissimus, (2) the loss of the caudal head of semitendinosus, and (3) the transference of the origins of both caudofemoralis and femorococcygeus from the vertebral column to the tuber ischii. Thus N. pudendus and the nerve to obturator internus pass deep to M. femorococcygeus in *Tupaia*, but do not do so in *Macroscelides*.

The present investigation has shown that in a large number of mammals there is present a muscle showing the characteristic features of M. femorococcygeus in *Tupaia* (pp. 394, 405). It is therefore inferred that *Macroscelides*[1] has been specialised in the acquisition of an ischial origin for M. femorococcygeus. This view finds support in the considerations that (1) its habits are specialised, (2) the origin is found on the tuber ischii in a few other mammals (including the gorilla, chimpanzee (fig. 10 C), gibbon, *Loris grac.* and *Erinaceus*), (3) the similar transference in a few mammals of the origin of M. caudofemoralis from the caudal vertebrae to the tuber ischii (*vide infra*, pp. 388, 397), (4) the evidence of specialisation in *Macroscelides*[1] presented in the loss of tenuissimus and of the caudal head of semitendinosus, as well as in certain other features which are beyond the scope of this paper.

*M. caudofemoralis.* The muscles so identified in *Tupaia* and *Macroscelides* agree in being placed between Mm. femorococcygeus superficially and Mm. quadratus femoris, adductores and semimembranosus on the deep aspect. They have similar insertions, in *Macroscelides* somewhat restricted in extent. In each animal the muscle is deep (ventro-medial) to the tibial and peronaeal nerves and the sural cutaneous elements in each of them, and deep also to the nerve to M. femorococcygeus. The nerve supplying the muscles identified as "caudofemoralis" agrees in *Tupaia* and *Macroscelides* in passing between Mm. femorococcygeus and quadratus femoris. The caudofemoral muscles are in each animal superficial to the nerves to biceps, semitendinosus and semimembranosus (the nerve to the first of these separating M. caudofemoralis from the two last)[2]. Differences in the relations of the muscles appear to be due to (1) loss in *Macroscelides* of certain muscles, mentioned above (figs. 4 and 5), and (2) the ischial origin of the muscle in question in *Macroscelides*[1],

[1] *Elephantulus* is similar.

[2] This account of the innervation of biceps differs from that of Leche (*vide infra*).

whereas in *Tupaia* this is caudal. Thus N. pudendus (with N. perinaealis) and the nerve to the obturator internus passing medially to the tuber ischii in *Macroscelides* come into no close relation to M. caudofemoralis. In *Tupaia*, as in *Macroscelides*, N. cut. femoris posterior passes superficially to this muscle, but the other two nerves lie deep to it.

It will be shown that among the more primitive mammals a muscle presenting features similar to those of the caudofemoralis of *Tupaia* is of widespread occurrence. The inference that the ischial origin in *Macroscelides* is the more specialised is supported by considerations similar to those already advanced for M. femorococcygeus. The ischial head of origin has been found in a few other mammals only, viz. in *Tarsius spectr.* (Appleton, 1921, Plate IV, and p. 468), in some Lipotyphlous Insectivora and in *Manis*. Parsons' descriptions of Rodentia point to its occurrence in various families of that order. Inasmuch as the thigh structure of *Hapale* (fig. 8) approximates closely to that of *Tupaia*, it will be seen that *Macroscelides* differs from *Tupaia* in regard to its M. caudofemoralis in a manner similar to that in which *Tarsius* differs from *Hapale*. In *Macroscelides*, however, as already mentioned, M. femorococcygeus has also acquired an ischial origin, but this is not so in *Tarsius* (Appleton, 1921, p. 467).

*The innervation of M. biceps in Menotyphla* (figs. 4 and 5). The nerve supplying this muscle intervenes between M. caudofemoralis and Mm. semimembranosus and semitendinosus (caput isch.). In *Tupaia* it comprised three bundles associated with the nerve to semitendinosus and less closely associated with that to semimembranosus, the series of nerves forming a trunk described by Leche as "4 i." This account of the innervation of biceps differs from that of Leche (1883, p. 44), who describes it as coming from the nerve "4 k," while he definitely states that "4 i" does not supply biceps. Le Gros Clark (1924) has described a nerve supply to biceps in *Tupaia* in its proximal part from N. tibialis and distally from N. peronaeus (where these nerves form a part of the sciatic nerve), apparently corresponding to Leche's nerves "4 k" and "4 i." The innervation from "4 i" was probably overlooked by Leche owing to its concealed position. I have been unable to detect any branch to the distal part of biceps from N. ischiadicus after this nerve has passed dorsally to M. caudofemoralis[1]. It is possible that both Leche and Le Gros Clark have regarded one of the above-mentioned sural branches of the peronaeal nerve (probably N. surae dorsalis, p. 387) as a motor twig ("4 k") to biceps, inasmuch as they have not described these cutaneous nerves.

Between the nerves named "4 k" and "4 i" by Leche there are two topographical differences which are significant for the study of comparative myology. Between them are situated both the caudofemoralis and tenuissimus muscles. This arrangement is general throughout Mammalia (except when one of these muscles is absent), and corresponds to the relations presented

[1] This statement refers to my dissections of *Ptilocercus* and *Elephantulus* as well as to those of *Tupaia* and *Macroscelides*.

by similar muscles in other classes of Tetrapoda (e.g. by Mm. femorocaudalis and iliofibularis respectively in *Sphenodon*, p. 379, cf. figs. 1 and 3, and the table of synonyms, p. 434).

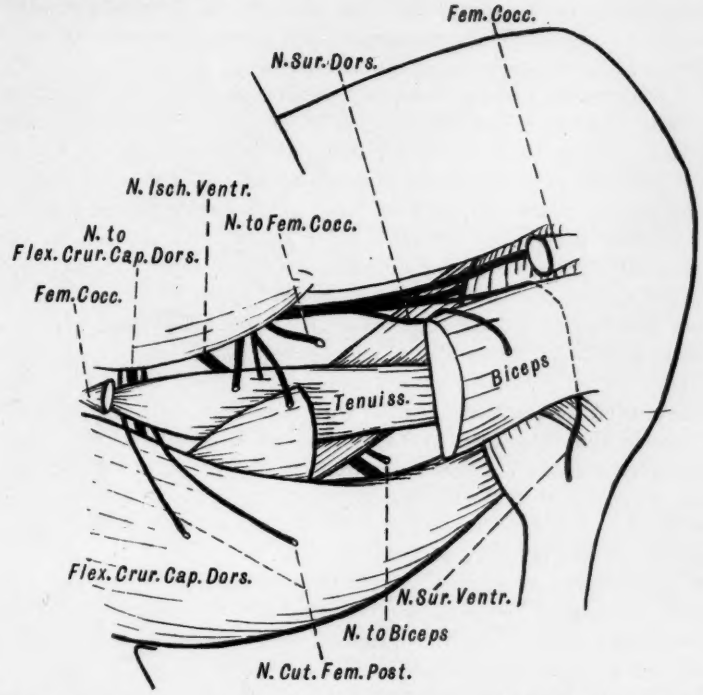


Fig. 6. *Talpa eur.* Right thigh, ×3½. Position and dissection similar to that of *Tupaia* in fig. 4, p. 385, except that M. biceps is divided and the dorsal head of M. flexor cruris has not been divided.

The structural pattern of the primitive eutherian thigh is preserved almost unaltered despite the enormous enlargement of certain muscles, especially biceps and the dorsal head of M. flexor cruris. One modification of the musculature, the transference of the origin of M. caudofemoralis from the tail to the tuber ischii, involves a failure of some nerves to come into direct relation with it, as in *Macroscelides* (fig. 5). The extensive skin area of the lateral thigh region is innervated by Nn. cut. femoris posterior and cut. surae lateralis, each of which is represented by more than one large bundle. As in Amniota generally, the nerves to M. flexor cruris (including the nerve supply of biceps and of the dorsal head) pass ventrally to M. caudofemoralis, N. cut. femoris posterior passes ventrally to M. iliofibularis, but N. cut. surae lateralis (comprising Nn. surae dorsalis and surae ventralis) and N. ischiadicus dorsalis (of which the nerve to femorococcygeus is a part) pass dorsally to it.

M. caudofemoralis is the unnamed muscle deep to tenuissimus.

**Lipotyphla** (fig. 6). Examples of *Talpa eur.* and *Erinaceus eur.* have been dissected. Leche stated that M. caudofemoralis is absent from all the Insectivora he examined except *Tupaia* and *Macroscelides*. I have, however,

not found it possible to differentiate between the M. praesemimembranosus of *Talpa* and *Erinaceus* and the caudofemoralis of *Macroscelides* (which has already been homologised with that of *Tupaia*). It appears from Leche's account that in most Lipotyphla there has occurred a transference to the tuber ischii of the origin of M. caudofemoralis such as has undoubtedly occurred in *Talpa* and *Erinaceus* as well as in *Macroscelides*.

The relations claimed by Leche for "praesemimembranosus" (1883, p. 94) are equally true for the caudofemoralis of Menotyphla. Proximal attachments have been already discussed; distal attachments on the shaft of the femur present relations to neighbouring muscle attachments which are very much alike (cf. Leche's figs. 60, 63, with fig. 5 *supra*). It may be further pointed out that the relations already established for Menotyphla between M. caudofemoralis and nerves, viz. Nn. tibialis and peronaeus, surae dorsalis and surae ventralis (p. 387), and to the nerves to hamstring muscles (semitend., semimembr. and biceps), are identical with those presented by M. praesemimembranosus in *Erinaceus* and *Talpa*, and Leche's figures show that the same may be said for M. praesemimembranosus in certain other Lipotyphlous Insectivora (cf. *Chrysochloris*, fig. 93, with *Erinaceus*, fig. 75, Leche, 1883)[1]. The muscle thus identified in Lipotyphla as M. caudofemoralis (Leche's praesemimembranosus) differs from that of *Tupaia* in just those features which are incidental to the transference of its origin to the tuber ischii, as in *Macroscelides*. For example, the nerve to the dorsal head of M. flexor cruris caput dorsale does not pass ventrally to it (fig. 6).

It is significant, in connection with the identification here made between Leche's lipotyphlous praesemimembranosus and the menotyphlous caudofemoralis that Leche claimed a praesemimembranosus exclusively in those Insectivora in which he described caudofemoralis as absent.

Leche's account of the innervation of M. biceps in Lipotyphla requires amendment. Two nerves pass to it in *Talpa* from the hamstring nerve (Leche's "4 i"), which travels ventro-medially to M. caudofemoralis and supplies also the Mm. semimembranosus and semitendinosus caput ischiale. No twigs were found to supply it from N. surae dorsalis or N. surae ventralis. Now Leche described an additional innervation of M. biceps through a distal nerve "4 k," travelling dorsally to M. caudofemoralis as a part of N. ischiadicus. This is probably N. surae dorsalis whose cutaneous character he overlooked. In *Talpa* there are, besides the Nn. surae dorsalis and surae ventralis (resembling those of *Tupaia*, p. 386), four other cutaneous nerve bundles distributed to the extensive region over the greatly enlarged Mm. flexor cruris caput dorsale (semitendinosus caput caudale) and biceps (fig. 6). Two pursue a course like N. cut. femoris posterior ventrally to tenuissimus and then between femorococcygeus and biceps; they pass medially to the tuber ischii

[1] Leche's fig. 90 of *Erinaceus* appears to show the nerve "4 i" in incorrect relation with "M. praesemimembranosus," i.e. M. caudofemoralis. But in his fig. 75 and his statement on p. 44 there is agreement with my finding.

in company with the large nerve to M. semitendinosus caput caudale (Leche's "4 d"), like the single N. cut. femoris posterior found in *Macroscelides*. The other two present features suggesting separated portions of N. surae dorsalis.

*Résumé. Concerning Mm. caudofemoralis, femorococcygeus and biceps, and the associated nerves in Insectivora.*

The conclusions of Leche have been found to require modification. The "praesemimembranosus" of that author has been identified with his "caudofemoralis," and the latter name has been adopted for use throughout Insectivora (and mammals generally, p. 411). The lipotyphlous praesemimembranosus of Leche has been found to differ from the muscle so named in the cat (cf. fig. 12 I) and from the "ischiocondyloideus" of various Primates (with which muscles it was compared by Leche, 1883, p. 95), inasmuch as these are parts of the semimembranosus musculature, situated medially to the nerves to Mm. biceps and semitendinosus and medially also to M. caudofemoralis in such Carnivora and Primates as possess it (e.g. *Lutra*, fig. 7, and *Lemur*, Appleton, 1922, p. 301). M. biceps is found to be innervated solely through the main hamstring nerve trunk (Leche's "4 i"), which passes ventro-medially to M. caudofemoralis. It is thus found to be a part of the ventral or hamstring musculature, and not of the dorsal musculature, as Leche supposed (*vide* p. 424 *infra*). Leche's account of Insectivora would lead to the inference that Menotyphla and Lipotyphla differ (*a*) in the occurrence of a praesemimembranosus and a caudofemoralis, and (*b*) in the mode of innervation of biceps. But in none of these features is it found possible to maintain a distinction between these groups of Insectivora. The structure of the post-axial region of the thigh and buttock presents no difficulty to Carlsson's proposed separation of the Macroscelididae from the Tupaiidae, and her association of the former with the Lipotyphla.

The innervation of M. caudofemoralis in Insectivora is found to be through a nerve passing between Mm. tenuissimus and the ischially-attached hamstrings (M. flexor cruris cap. ventr.); it is closely associated at first with N. tibialis and with the nerves to M. flexor cruris cap. ventr. (biceps, semitendinosus and semimembranosus); it leaves N. tibialis in company with the nerve bundles to the last-named muscle mass in *Tupaia*, *Macroscelides* and *Chrysochloris*, but more proximally than those bundles in other Insectivora.

### (*b*) *Comparison of Insectivora with other Mammalia.*

(Cf. figs. 4, 5 and 6 with figs. 7–15.)

The arrangement of structures already described in the thigh of *Tupaia pict.* and present also in a modified form in *Macroscelides* and other Insectivora, presents a close resemblance to that found in other mammals, and is especially like that in the more primitive ones. For example, in *Hapale jacch.* among

Primates (fig. 8), in *Genetta* and *Lutra* (fig. 7) among Carnivora, and in *Erethizon* (fig. 15) and *Mus* among Rodentia, the topographical relations of muscles to one another, to nerve bundles and the distributions of nerves agree very closely with those in *Tupaia*. Monotremata (fig. 14) and Marsu-

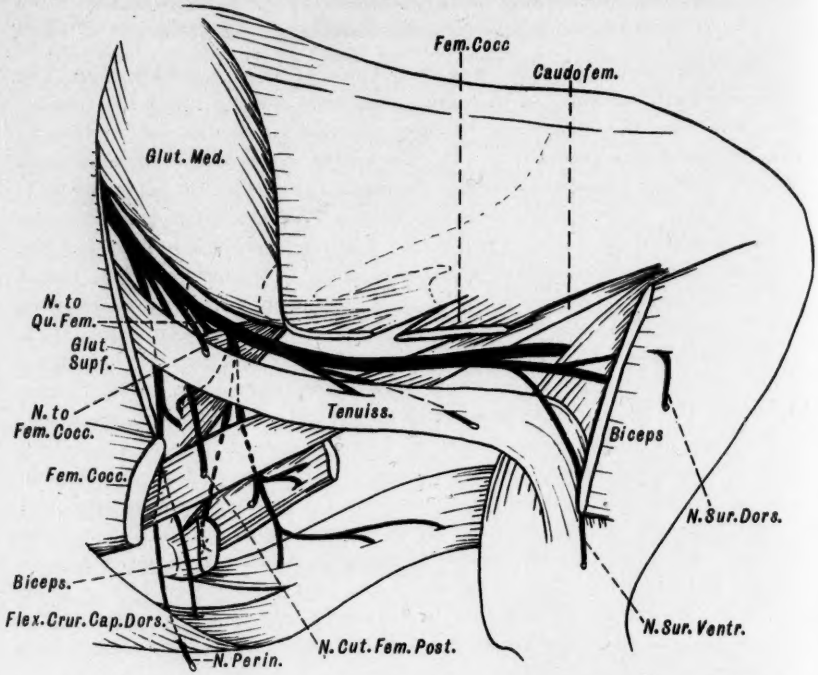


Fig. 7. *Lutra vulg.* Right thigh, $\times \frac{3}{4}$. Position and dissection similar to that of *Tupaia* in fig. 4, p. 385, except that biceps has been removed in part, and the dorsal head of M. flexor cruris has not been divided. The relations of nerves to muscles (of which a primitive eutherian arrangement is retained) are similar to those found in Tetrapoda generally, excepting the passage of a nerve *through* M. iliofibularis and of N. perinaealis through M. flexor cruris cap. dors. N. ischiadicus ventralis is represented by (1) a large trunk supplying the ventral head of M. flexor cruris, (2) a nerve accompanying Nn. perinaealis and pudendus, and supplying the dorsal head of flexor cruris, (3) the nerve to quadratus femoris, (4) the nerve to obturator internus. All these pass ventrally to M. caudofemoralis. N. ischiadicus dorsalis is represented by (1) the nerve to tenuissimus, (2) N. glutaeus anterior (sup.), (3) N. glutaeus posterior (inf.), (4) the nerve to femorococcygeus. N. cutaneus surae lateralis is represented as in many other Eutheria by two nerves (Nn. surae dorsalis and ventralis); it passes dorsally to M. iliofibularis.

palia (fig. 11) present the same arrangement of structures, though in the former the enormous size of M. flexor cruris cap. dors. (cf. the caudal head of semitendinosus in Insectivora, *vide* p. 420) and the loss of tenuissimus, and in marsupials (fig. 11) the proximally displaced site of insertion of

M. caudofemoralis, have in the past obscured the close resemblance of the three mammalian sub-classes.

Among Eutheria there has been a tendency, with specialisation of the limbs, to the loss of one or more of the muscles caudofemoralis (fig. 10 D), tenuissimus (figs. 5 and 8), and flexor cruris cap. dors. (often described as the caudal head of semitendinosus) (fig. 10). Failure to recognise them when

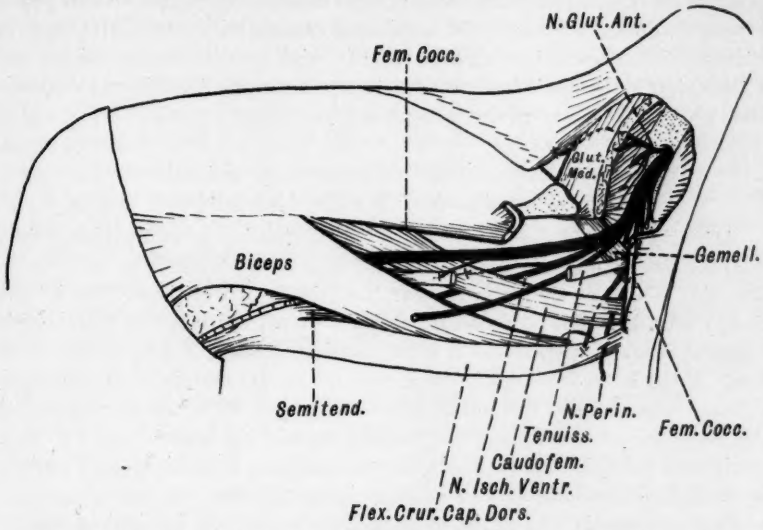


Fig. 8. *Hapale jacch.* Left thigh, ×2. Position and dissection similar to that of *Tupaia*, fig. 4, p. 385, except that the dorsal head of M. flexor cruris has not been divided. Mm. tensor fasciae latae and femorococcygeus are very incompletely differentiated from M. glutaeus superficialis, while other primitive eutherian features exhibited by *Tupaia* are also retained. Mm. caudofemoralis and tenuissimus present the relations to nerves which are characteristic of Tetrapoda generally (cf. fig. 1). N. ischiadicus dorsalis is represented by the anterior and posterior glutaeal nerves (whose distribution is indicated), and by the nerve to tenuissimus. The tetrapod, N. pudendus, is represented by the "N. pudendus," by the nerve to M. caudofemoralis (which has become bound up with N. ischiadicus ventralis), and by N. perinaealis. The dorsal head of M. flexor cruris is supplied by N. ischiadicus ventralis as in all Amniota (figs. 3 and 13). N. perinaealis, as an individual variation in *Hapale jacch.*, may pierce M. caudofemoralis and the dorsal head of M. flexor cruris (cf. fig. 7); the condition is shown in this figure. In other individuals examined it passed deep to both muscles, as in Amniota generally.

present has been responsible for many misleading descriptions to be found in the literature of mammalian myology (pp. 395, 406, 411, 430). Errors may also be traced to the varied mode of union of the dorsal with the ventral head of M. flexor cruris (p. 424) and to the confusion by various writers of parts of the glutaeal (p. 406) and adductor (p. 431) musculature with "biceps" and "(pre-)semimembranosus" respectively.

In mammals the sequence of structures in the proximal part of the thigh

from the dorsal to the ventral aspect is the same as that found in the Insectivora (with modifications due to reduction of the part or whole of certain muscles), viz. Mm. glutaei and muscles derived therefrom (tensor fasciae latae, femorococcygeus, pyriformis, scansorius, glutaeus ventralis), Nn. surae dorsalis and ventralis[1], and N. peronaeus; M. tenuissimus with its nerve; N. cut. femoris posterior and Nn. tibialis and cut. surae medialis; M. caudofemoralis with its nerve; M. flexor cruris cap. dors.; N. perinaealis; M. biceps with its nerve, M. semitendinosus with nerve, M. semimembranosus with nerve; Mm. gemelli, obturator internus and quadratus femoris with nerves. In the distal part of the thigh M. biceps is interposed between Nn. surae dorsalis and ventralis[2] when both of these nerves are present (fig. 10).

*Notes for guidance in the dissection of the glutaeal region and adjacent parts of the thigh, in Mammalia.*

Attention should first be given to the distinction of superficial glutaeal from hamstring musculature. In the interval between them N. cut. femoris posterior comes to the surface, near the middle of the thigh. The interval should then be followed medially, and the hamstring muscles examined for a caudal head. N. perinaealis is found passing through or deep to the caudal head. If the latter is absent it emerges at the caudal margin of the superficial glutaeal musculature (frequently represented by a M. femorococcygeus). At this stage the nerve supply of the "caudal head of the hamstrings" (M. flexor cruris cap. dors.) is found. In the interval between Mm. biceps and glutaeus superficialis the sciatic nerve should be inspected, and the nerve to femorococcygeus secured; the origin of sural nerves from N. ischiadicus may be searched for at this stage. If a tenuissimus is present it is recognised by general relations, and more definitely by its relation to N. cut. femoris posterior (to which it is dorsal). If a M. caudofemoralis is present it will be found to intervene between the main sciatic nerve (Nn. tibialis and peronaeus) and the nerves to the hamstring muscles; N. perinaealis may be expected to be deep to it, but N. cut. femoris posterior superficial to it.

(*c*) *Absence of muscles in certain mammals.*

Reference has already been made (p. 393) to the frequency with which Mm. caudofemoralis, tenuissimus and flexor cruris cap. dors. are absent in mammals, mainly in the more specialised orders and members of orders. The distinctive features of the courses of certain nerves become obscured in these instances. Thus, when M. tenuissimus is absent, a valuable criterion for the distinction of N. cut. femoris posterior from Nn. surae dorsalis and ventralis is wanting (figs. 5 and 8). An approximate distinction is however

[1] In some mammals only one of these is present (cf. pp. 386, 398). These nerves are regarded as together constituting the mammalian representatives of the tetrapod N. cutaneus surae lateralis.

[2] See footnote on p. 376.

offered by the distribution of these nerves, mainly to the thigh and shank respectively. When, again, M. caudofemoralis is absent (fig. 10 D) the distinction between Nn. cut. femoris posterior and perinaealis is less clearly defined; they have indeed come to form, in Man and the giant anthropoids (except *Simia*), a single trunk, the perinaeal nerve being described as a branch of the former. When, further, as in many Primates and in Artiodactyla, both the muscles caudofemoralis and tenuissimus are wanting, the courses of a number of nerves have become similar, viz. Nn. ischiadicus dorsalis (represented by glutaeal nerves), peronaeus, tibialis and ischiadicus ventralis (represented by nerves to hamstrings, quadratus femoris, obturator internus and flexor cruris caput dorsale); and the cutaneous nerves surae superficialis and profundus, cutaneus femoris posterior and perinaealis. Comparison, however, of such Primates with their relatives (cf. figs. 10 D, 8, 5 and 4) which happen to be in possession of one or other of Mm. caudofemoralis and tenuissimus, suffices to establish the identity of the nerves, and assists in the correct homologisation of the musculature by which they are innervated. Thus the distinction[1] between the "ischio-femoralis" of the orang-outan and that of the gorilla and chimpanzee (p. 425) appears justified despite the absence of both Mm. tenuissimus and caudofemoralis.

### (*d*) *Comparison of Mammalia with other Classes of Tetrapoda.*

(Cf. figs. 1 and 3 with figs. 7, 8, 14 and 15.)

The arrangement of structures in the thigh and buttock of Insectivora, summarised in the previous section, agrees closely with that which has been shown to exist in the Amphibia, Reptilia and Aves. The names, however, which are commonly employed in descriptive anatomy, obscure this similarity. As already indicated, the structural arrangement of Insectivora closely resembles that of the other mammals.

The name "tenuissimus" is employed in mammalian literature by Leche and others to describe a muscle presenting features like the iliofibularis of other tetrapod classes.

The name "caudofemoralis" was employed by Leche to describe an insectivore muscle which reproduces the relations of the reptilian femorocaudalis (Frets) and its equivalents in amphibians and birds. Given these identifications, the relations of the principal nerves to muscles are the same in mammals as in other groups, as illustrated by the summaries for dorsoventral sequence of post-axial structures provided for Insectivora (p. 394) and Urodela (p. 376).

Brief consideration will be given below (pp. 401–426) to the muscular changes involved in the representation in mammals by biceps, semimembranosus and semitendinosus of the reptilian caput ventrale of M. flexor cruris, those involved in the specialisation and subdivision of the reptilian

[1] By Fick and Kohlbrügge.

iliofemoralis and ischiotrochantericus (Osawa), and the not infrequent persistence in mammals of the reptilian femorocaudalis (Frets), iliofibularis and flexor cruris caput dorsale.

Ventrally to Mm. tenuissimus and caudofemoralis in mammals there are nerves which are identified as constituent bundles of Nn. ischiadicus ventralis and pudendus (pp. 372, 374); their course and distribution resemble those which in reptiles pass ventrally to Mm. iliofibularis and "femorocaudalis" (i.e. the tetrapod caudofemoralis) (figs. 1, 8 and 13).

The N. ischiadicus ventralis, which in reptiles comprises one large trunk destined for both ventral and dorsal heads of M. flexor cruris (p. 381) and one or more smaller ones for the short deep musculature (viz. ischiotrochantericus and in some reptiles parts of the pubo-ischio-femoralis externus and ischio-femoralis of Gadow), is represented in mammals by several nerve bundles. For the distinction of these bundles from those belonging to N. pudendus we are dependent on a study of their distribution, owing to the similarity of course pursued by Nn. ischiadicus ventralis and pudendus relative to muscles and bone (cf. figs. 1, 7 and 8).

N. ischiadicus ventralis (cf. fig. 7) in mammals comprises (*a*) the nerve to which Leche applied the term "4 i" in Insectivora (p. 391 *supra*), supplying M. flexor cruris cap. ventr. (i.e. Mm. biceps, semitendinosus and semimembranosus, but without their so-called "caudal heads"), (*b*) the nerve to M. flexor cruris cap. dors. (caudal head of hamstring musculature), which generally keeps close company with the cutaneous element of N. pudendus (fig. 7), and (*c*) the nerves to short deep muscles, represented in Monotremata by the nerve to M. ischiotrochantericus (Pearson's "obturator B"), but in most mammals by separate nerves to quadratus femoris and obturator internus (and associated gemelli). In Monotremata and Marsupialia (fig. 11), the first and last of these (*a* and *c*) leave N. tibialis as a single trunk to which Cunningham with some reluctance applied the name "nerve to the hamstrings," recognising the inclusion in this nerve of bundles destined for the deep muscles. Frets (1909, p. 90) named the same nerve N. ischiadicus ventralis, but this nerve differs from that to which he gave this name in *Sphenodon* in the absence of any component destined for M. flexor cruris cap. dors., and in the inclusion of bundles for short deep muscles. In this paper the term N. ischiadicus ventralis has been applied (p. 372) to a single comprehensive nerve stem destined for ventral thigh muscles and skin in Urodela (fig. 1); in other groups it has been found that certain of its constituent bundles, most commonly those destined for the short deep musculature, leave the main sciatic stem independently.

One point of difference in the N. ischiadicus ventralis of mammals deserves note: no cutaneous element comparable with the N. cut. femoris ventralis of other tetrapod classes is known to me in mammals.

N. pudendus is represented in mammals, as in birds, by two widely separated nerves. The cutaneous nerve already described in mammals as

N. perinaealis presents a course[1] and distribution in the Monotremata (fig. 14), Marsupialia (fig. 11), Rodentia (fig. 15), Carnivora (fig. 7), Insectivora (figs. 4 and 5), and Primates (figs. 8 and 10), so far examined, which identify it with the nerve which has been so termed in other tetrapod classes (pp. 374, 377, 382, 383). But with the reduction of the great caudofemoral retractor musculature of the more primitive Tetrapoda and its inclusion for the most part in the thigh (fig. 9), the nerve to M. caudofemoralis itself has become more distally situated and more closely associated with the branch of N. ischiadicus ventralis destined for M. flexor cruris cap. ventr. (figs. 5 and 8), or occasionally with that for the dorsal head (fig. 15). The transference in certain mammals of the origin of M. caudofemoralis from the tail to tuber ischii is responsible in these instances (e.g. Macroscelididae and *Tarsius*[2]) for its failure to present the customary relations to the more proximally placed nerves, viz. N. pudendus, and nerves to obturator internus, quadratus femoris, and flexor cruris cap. dors. (*vide* p. 388).

In mammals, then, both the nerve trunks, ischiadicus ventralis and pudendus, have undergone disintegration, and owing to the similarity of their courses the constituent bundles of these nerves require reference to their distribution for their distinction. Thus it has been concluded that a part of N. perinaealis has become closely associated in many mammals (fig. 7) with the nerve to M. flexor cruris cap. dors. (a component of N. ischiadicus ventralis), while the nerve to M. caudofemoralis has also become closely associated with the nerve bundles destined for M. flexor cruris (usually the ventral head).

The relations (to Mm. caudofemoralis and tenuissimus) and the distribution of N. peronaeus and Nn. surae dorsalis and ventralis, point to these nerves being the mammalian representatives of the N. peronaeus and N. cutaneus surae lateralis of other tetrapod classes. Similarly the glutaeal nerves present courses and distribution showing them to be components of the N. ischiadicus dorsalis; and a study of the musculature (p. 406 *infra*) points to their being differentiated from the nerve to M. iliofemoralis of pro-mammalian reptiles (cf. figs. 1, 9 and 12).

Inasmuch as M. tenuissimus presents every feature needed for its identification with the reptilian M. iliofibularis, the nerve to this muscle (fig. 9) and the glutaeal nerves together correspond to the N. ischiadicus dorsalis already described in other classes.

In mammals N. peronaeus and Nn. surae dorsalis and ventralis pass dorsally to M. caudofemoralis and round the pre-axial side of tenuissimus, just as in reptiles they[3] pass dorsally to M. femorocaudalis and pre-axially

[1] This nerve pierces the dorsal head of M. flexor cruris in some mammals, e.g. *Lutra vulg.* and in one of the examples of *Hapale jacch.*; in the latter instance it was found to pierce M. caudofemoralis also. These features are divergences from the usual tetrapod relations.

[2] Appleton, 1921, Plate IV, and p. 468.

[3] Represented by N. peronaeus and N. cutaneus surae lateralis.

to M. iliofibularis. The glutaeal nerves do not as a rule reach sufficiently far to show these relations clearly, though the relations are evident when N. glutaeus posterior becomes extended distally for the supply of M. femorococcygeus. The nerve to tenuissimus (figs. 6, 7, 8, 15) passes dorsally to M. caudofemoralis in those mammals which possess these muscles, just as in reptiles that to iliofibularis passes dorsally to the femorocaudalis (fig. 3).

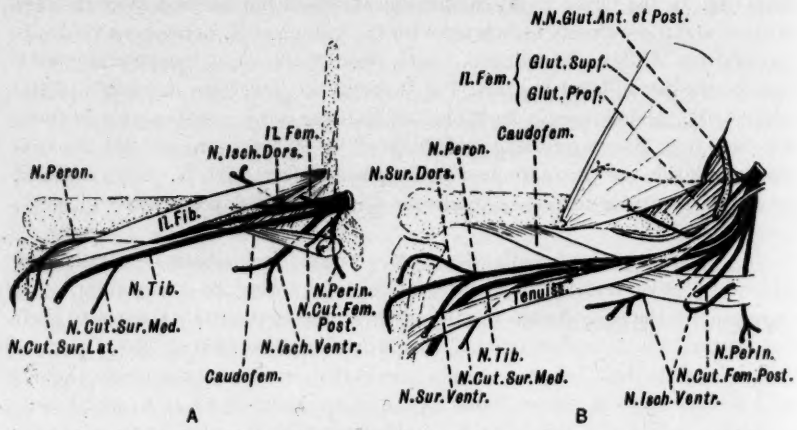


Fig. 9. Diagram showing the principal metazonal nerve-trunks of the thigh in the frogs (Salientia) and mammals. (A) Salientia, (B) Mammalia.

They alike show segregation of nerve bundles to dorsal thigh muscles (N. ischiadicus dorsalis) from the nerves to the dorsum of the leg and foot (N. peronaeus), cf. fig. 1. In both groups reduction of the primitive caudofemoral retractor musculature has occurred; but in mammals the vestige is situated mainly in the thigh and the nerve (a constituent of N. pudendus) travels into the thigh in company with N. ischiadicus ventralis. In mammals the nerve to iliofibularis (tenuissimus) is associated with N. peronaeus for some distance into the thigh, and is widely separated from the remainder of N. ischiadicus dorsalis (viz. Nn. glutaei anterior et posterior).

In both groups M. flexor cruris has become greatly elaborated; mammals have however retained a more or less vestigial representative of the Amniote dorsal head, which is innervated from a recurrent branch of N. ischiadicus ventralis (cf. figs. 3, 14 and 15). N. cutaneus femoris posterior is large in mammals as in other Amniota, small in frogs as in Urodela. N. cut. surae lateralis is often represented by two bundles in Mammalia (p. 394).

The relations of nerves to Mm. iliofibularis and caudofemoralis conform to the general structural pattern of Tetrapoda (cf. fig. 1).

In mammals N. peronaeus is closely associated with N. tibialis till near the knee; in this they resemble the frogs, birds and reptiles more closely than the urodeles in whom a N. fibularis is compounded from N. peronaeus and N. ischiadicus dorsalis (cf. figs. 1 and 9).

The two cutaneous nerves representative of the reptilian N. cut. surae lateralis have been found among Rodentia, Primates and Carnivora as well as in Insectivora, separated by the whole or part of M. biceps cruris (i.e. a part of M. flexor cruris caput ventrale, p. 425). In *Perameles* and *Canis*

I could only find one such nerve; in the former it pierced biceps, in the latter it was placed like a N. surae ventralis (described by Bradley by the name of "N. cutaneus surae lateralis"). In Macroscelididae the only one of these nerves present is situated like a N. surae dorsalis.

N. tibialis passes dorsally to M. caudofemoralis, but remains ventral to M. tenuissimus (iliofibularis), as in other tetrapod classes. It again provides a cutaneous element which is identified as a N. cut. surae medialis. The latter has a distribution similar to that in other tetrapod classes, but is peculiar in passing medially to the insertion of a part of M. flexor cruris (viz. M. biceps), a feature which appears attributable to the transference of this insertion to the lateral side of M. gastrocnemius (p. 424). The distal innervation of M. flexor cruris cap. ventr. through a nerve passing with N. tibialis dorsally to M. femorocaudalis, which has been found in certain Amphibia, reptiles and birds (pp. 374, 382, 383), is perhaps represented in mammals also, for in *Dasyurus mac.* I have found such nerve bundles reaching the distal parts of M. semitendinosus in addition to the innervation through N. ischiadicus ventralis. Cunningham evidently observed a similar distal innervation in certain Marsupialia (1881, p. 271).

A N. cut. femoris posterior has been found in all mammals examined. It is identified by its distribution and by its course between Mm. iliofibularis (tenuissimus) and caudofemoralis with the nerve to which this name has been applied in other tetrapod classes. The nerve is peculiar in *Meles tax.* and *Lutra vulg.* in its penetration of M. tenuissimus.

The relations of cutaneous nerves to muscles in mammals are therefore as follows: (1) *dorsal* to both caudofemoralis and tenuissimus[1], N. cutaneus surae lateralis, represented in some mammals by the Nn. surae superficialis and profundus (separated distally by the whole or part of biceps); (2) *between* caudofemoralis and tenuissimus, Nn. cut. femoris posterior (which emerges between femorococcygeus and biceps) and cut. surae medialis, the latter separated from the former by biceps; and (3) *ventral* to both caudofemoralis and tenuissimus, N. perinaealis, separated from N. cut. femoris posterior by caudofemoralis. The relations of muscular and cutaneous nerves to the thigh muscles of Mammalia are like those described in other tetrapod groups, save the relations of the distal part of biceps to adjacent nerves (cf. pp. 375, 379, 420 and 424).

### 6. Review of the tetrapod metazonal nerves.

(Fig. 1, p. 373, and fig. 9, p. 398.)

In Urodela, Salientia, Lacertilia, Chelonia, Crocodilia, Aves, Monotremata, Marsupialia and Eutheria, it has been found that the muscular and cutaneous nerves reaching the hind-limb on the caudad side of the os coxae fall into four categories differing in their course relative to the thigh muscles and possessing characteristic distributions.

[1] I.e. the tetrapod iliofibularis (cf. pp. 402, 425).

A: N. ischiadicus dorsalis is distributed to dorsal thigh muscles; it passes dorsally to M. caudofemoralis and round the pre-axial (medial) side of M. iliofibularis.

B: N. peronaeus (including a N. cutaneus surae lateralis) is distributed to muscles and skin on the dorsum of the shank and foot; it pursues a course similar to that stated for N. ischiadicus dorsalis (A).

Y: N. ischiadicus ventralis (including a N. cutaneus femoris ventralis) and N. pudendus (including a N. perinaealis) pursue similar courses ventrally to M. caudofemoralis (and iliofibularis); the former is distributed to ventral thigh musculature and skin, the latter to ventral musculature which is usually partly within the tail, and to skin near the anus.

Z: N. tibialis (including a N. cutaneus surae medialis) is distributed to muscles and skin on the ventral side of the shank and foot (and to the distal part of the ventral thigh muscles in some groups, p. 399); it passes dorsally to M. caudofemoralis but ventrally to M. iliofibularis. In the thigh a cutaneous nerve (N. cutaneus femoris posterior) pursues a similar course relatively to Mm. caudofemoralis and iliofibularis.

In Urodela, A and B form a single trunk which leaves the others in the proximal part of the thigh; in all other groups N. peronaeus (B) does not accompany A when the latter leaves N. tibialis (Z), but forms with Z a single trunk, commonly described as the sciatic, which is thus distributed to both dorsal and ventral parts of the shank and foot. The urodele nerve supplying the dorsal parts of both thigh and shank is known as N. fibularis. The nerves for the ventral thigh structures (Y) leave those for the ventral aspect of shank and foot (Z) in the proximal part of the thigh in all Tetrapoda. Amniota present a muscle (M. flexor cruris caput dorsale) which is not found in Amphibia; it is associated at its insertion with the superficial ventral musculature (M. flexor cruris cap. ventr.) and is innervated from N. ischiadicus ventralis (Y) which, in order to reach it, is prolonged round the latero-distal margin of M. caudofemoralis.

Either or both Mm. caudofemoralis and iliofibularis may be absent in mammals, the former occasionally also in birds and frogs. A specialised derivative of M. caudofemoralis in the Amphibia (p. 409), the caudocrural muscle, is only rarely retained in modern frogs.

In the second part of this paper the muscle homologies which are involved in the foregoing study of structural pattern in the tetrapod thigh will be critically reviewed. References to the literature concerned will be found at the end of the second part of this paper.

# THE MUSCLES AND NERVES OF THE POST-AXIAL REGION OF THE TETRAPOD THIGH

## PART II

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## B. MUSCLES OF THE POST-AXIAL REGION OF THE TETRAPOD THIGH

The close resemblance which has been claimed in the first part of this paper for the courses of the principal nerves in relation to musculature throughout Tetrapoda has involved the homologisation of certain muscles in the various groups. It remains to examine the attachments and innervation of these muscles in order that the character of the inferences regarding muscle phylogeny involved in these conclusions may receive due examination.

### 1. M. iliofibularis

This name is applied to muscles of the various tetrapod classes which display certain characteristic relations to the following nerves: ischiadicus dorsalis, peronaeus, cut. surae lateralis, tibialis, and cut. femoris posterior. It intervenes between the first three and the last two of these. The muscles have been named by various writers as follows: Urodela—*ileofibularis*[1], de Man, 1873; *biceps*, Humphry, 1872: Salientia—*iliofibularis*, Gaupp, 1896, and Noble, 1922; *long head of biceps*, Nussbaum, 1898: Reptilia—*iliofibularis*[2],

[1] *Vide* footnote on p. 374.

[2] M. iliofibularis of Crocodilia consists, according to Gadow, of two parts. It has already been noted (p. 379) that his iliofibularis II presents relations to N. peronaeus showing it to be a differentiated part of M. extensor iliotibialis. Its insertion supports this inference. Gadow's iliofibularis I presents the characteristic relations of an iliofibularis (fig. 3 *supra*). Romer has reached the same conclusion from a consideration of the muscle attachments (1923, p. 537).

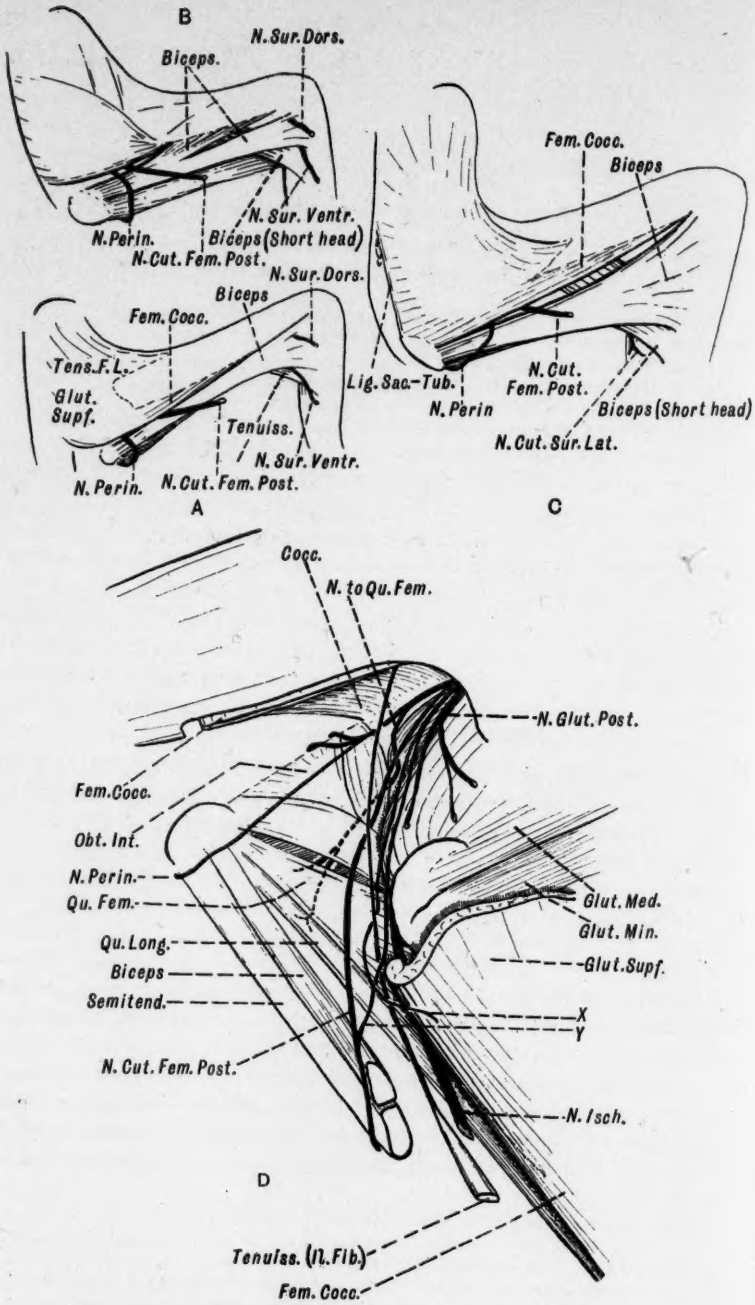


Fig. 10. For description see p. 403.

Fig. 10. A. *Cebus* (*mac.*?) × ⅔, B. *Simia sat.* × ⅔, C. *Anthropopithecus trogl.* × ¼: superficial views of the glutaeal and lateral thigh musculature (right). D. *Cebus* (*mac.*?) × 1½: deep dissection of the glutaeal region (right).

In the Primates here figured, Mm. caudofemoralis and flexor cruris caput dorsale are wanting, unlike the condition in *Hapale* (fig. 8). Thus no muscle intervenes between Nn. perinaealis and cut. femoris posterior. The relations of Nn. surales dorsalis and ventralis to the "short head of biceps" in *Simia* are shown (cf. figs. 10 A and B) to be like those of the same nerves to tenuissimus in *Cebus* (*vide* also p. 393). In many Primates (p. 405) the superficial glutaeal musculature has extended its insertion along the femur, but this part is not completely differentiated as a M. femorococcygeus (figs. 10 A, C and D). In the chimpanzee, gorilla and gibbon, and in *Loris gracilis* and *Perodicticus potto*, this musculature has extended its origin from the vertebral column to the tuber ischii with the formation of a fibrous arcade, the sacro-tuberous ligament. In the orang-utan, on the other hand, these extensions of the glutaeal musculature have not occurred; and catarrhine monkeys are similar to the orang. The so-called "ischiofemoral" muscle of *Simia* is shown not only by its innervation but also by its relation to N. cut. femoris posterior to be a part of M. biceps and phylogenetically distinct from the "ischiofemoral" or femorococcygeus of the other giant anthropoids (p. 425). In *Cebus* (fig. 10 D) the N. cut. femoris posterior is joined by a nerve *Y* whose course recalls that of a proximal branch of N. surae dorsalis (cf. *Talpa*, fig. 6); N. cut. femoris posterior has a recurrent branch *X* to the glutaeal region as in Man. The distal extension of the insertion of M. quadratus femoris (p. 426) in this new-world monkey parallels that in many Marsupialia (described by Cunningham, 1881, as "a part of adductor magnus"); the separate muscle thus formed will be distinguished by the name "quadratus longus."

Gadow, 1882: Aves—*iliofibularis*, Gadow, 1891; *biceps*, de Man, 1873: Mammalia—*tenuissimus*, Leche, 1883. The attachments and innervation of these muscles are consistent with their phyletic continuity. By Parsons and Klaatsch it has been claimed that the so-called "short head of biceps" in mammals has been derived in Edentata and Primates from M. tenuissimus[1]. Confirmation of this view, so far as Primates are concerned, is provided by a study of the cutaneous nerves; N. surae ventralis passes between the "long" and "short" heads of biceps in the orang-utan (fig. 10 B) and gorilla (Klaatsch), while in *Cebus* (fig. 10 A) it passes between Mm. biceps and tenuissimus (*seu* iliofibularis). In *Hapale* (fig. 8), *Lemur* and the catarrhine monkeys examined (in which no M. tenuissimus or "short" head is present), this nerve passed through the ventral (posterior) margin of biceps. In the chimpanzee, gorilla and gibbon I have been unable to trace the nerves surae dorsalis or surae ventralis in their customary primate relations (fig. 10). They have perhaps been displaced in relation to the restricted attachment of both long and short heads of biceps on the proximal end of the fibula, and are possibly represented by the human N. anastomoticus peronaeus and N. cutaneus surae lateralis respectively. These two nerves are thus together regarded as the equivalent of the N. cutaneus surae lateralis of other tetrapod classes (cf. fig. 10 C and Klaatsch's figures 2 and 3).

If reliance can be placed on the respective spheres of innervation of Nn. femoralis and ischiadicus dorsalis in superficial dorsal musculature, it

[1] No support has been found for those views which attempt comparison of the human "short head of biceps" with the ischial head of the biceps of various domestic animals (*vide* Martin, *Anat. d. Haustiere*, Stuttgart, 1919, Bd. I, p. 283, Bd. III, pp. 153, 255).

follows that M. iliofibularis became differentiated from this sheet independently in various groups (even among surviving orders of reptiles).

In most lizards and mammals (cf. p. 407) it would appear to have been formed from the whole metazonally-innervated part of the superficial dorsal sheet (Mm. extensor iliotibialis and rectus femoris being innervated solely from N. femoralis). But in frogs and urodeles, in birds, in *Sphenodon* and Chelonia, in Monitor lizards and in Crocodilia, M. iliofibularis does not comprise the whole of this metazonal musculature. From it there have also been derived Mm. cruralis and glutaeus in frogs, tensor vaginae in birds, ilioextensorius in urodeles and probably also Ogushi's "glutaeus maximus" in Chelonia; *Sphenodon*, Crocodilia and certain lizards present a diploneural M. extensor iliotibialis (Noble, 1922, p. 47; Gadow, 1882, p. 380). M. iliofibularis has thus perhaps included in some groups more, and in others less, of the metazonally-innervated superficial dorsal musculature.

The data summarised above might, of course, be interpreted as indicative of modifications of the respective shares taken in the innervation of superficial dorsal musculature by Nn. femoralis and ischiadicus dorsalis respectively (cf. also p. 416). The frequently-expressed view, that the mammalian biceps (ischial head) has been derived from the reptilian iliofibularis, is rejected (p. 425).

### 2. Mm. glutaeus superficialis, tensor fasciae latae and femorococcygeus

Gadow, Leche, and Gregory and Camp have suggested the derivation of these muscles from the superficial dorsal thigh musculature[1]. In this paper the view is advanced that they have been formed by differentiation of a M. iliofemoralis (deep dorsal musculature) of pro-mammalian reptiles.

Either view would be consistent with the homologies already proposed for nerves and muscles on the basis of the course of the main metazonal nerves, since Nn. ischiadicus dorsalis and peronaeus (the urodele N. fibularis) pass to the post-axial side of *both* the deep and the superficial dorsal musculature (excepting that part of the latter which forms M. iliofibularis). The mode of innervation also fails to distinguish between these hypotheses so far as Mm. glutaeus superficialis and femorococcygeus are concerned; the course of N. glutaeus posterior (*seu* inferior) (supplying these muscles in all mammals examined, cf. p. 421 *infra*) agrees with that of the bundles of N. ischiadicus dorsalis supplying *both* superficial and deep muscles (e.g. the urodele ilioextensorius and iliofemoralis).

Now a study of the glutaeal musculature itself points to the derivation of the superficial as well as the deep glutaeal muscles of mammals from a reptilian iliofemoralis. A comparison of members of the orders Insectivora, Rodentia, Carnivora, Marsupialia and Primates (figs. 4–8, 10, 11 and 15) points to the differentiation of Mm. tensor fasciae latae, glutaeus

[1] Leche, Parsons and various recent writers have supposed M. biceps femoris also to have been derived from this musculature. This view has been found untenable (p. 425).

superficialis (*seu* maximus) and femorococcygeus from a superficial sheet supplied by both the anterior and posterior glutaeal nerves (the former first piercing deep glutaeal musculature). Such a sheet occurs in *Cricetus, Cricetomys* and *Myodes* (according to Parson's data for Rodentia, 1896, p. 178), and in *Dasyurus* among Marsupialia. Most Primates present an early stage[1] in its differentiation. Catarrhine monkeys and *Simia* (fig. 10) present a single diploneural sheet attached on or about the third trochanter (or glutaeal fossa, Appleton (3), 1922, p. 296); Lemuroidea, *Hapale* (fig. 8), some Cebidae (Klaatsch, 1900), the gibbon, chimpanzee and gorilla show distal extension of its more caudad part, an incompletely differentiated M. femorococcygeus being thus formed (as Leche recognised in the case of the gorilla). In *Nycticebus tard.*, differentiation has proceeded further, for M. femorococcygeus is at its insertion quite distinct from the M. glutaeus superficialis. This distinction is not attained in *Loris grac.* (cf. *Cebus*, fig. 10). In Primates the more rostral part of the superficial glutaeal musculature is seldom clearly differentiated from the remainder to form a separate M. tensor fasciae latae as it does in Man. In this respect Insectivora are also primitive, for in *Tupaia* alone (cf. Leche, 1883) is it fairly distinct; in this order, on the other hand, a distinct M. femorococcygeus is of frequent occurrence (figs. 4, 5 and 6).

The older views of Gadow and Leche, according to which M. extensor iliotibialis of reptiles has become the superficial glutaeal musculature of mammals, would find their chief support in the widespread distribution in mammals of a distally-attached M. femorococcygeus. This muscle has a patellar attachment in various Macropodidae, in *Lepus* and many other Rodentia, in Artiodactyla and Perissodactyla (often described as "biceps"); it is attached to the patella or the distal end of the femur in many Carnivora (Parsons' "caudofemoralis" *seu* "agitator caudae") and to the distal part of the femur in Insectivora and in *Hyrax cap.* Leche was doubtless also influenced in his derivation of this glutaeal musculature from the superficial dorsal musculature by his faulty identification (cf. p. 420 *infra*) of the monotreme M. flexor cruris cap. dors. as a femorococcygeus with the inference that a distal attachment for this muscle is the more primitive condition (*vide* also Westling, 1890, p. 30). Such an attachment is, however, probably not primitive.

Careful examination of the lateral thigh musculature of many mammals, with a view to the distinction of glutaeal from biceps musculature, has satisfied me that a localised attachment of the superficial glutaeal musculature in the neighbourhood of the third trochanter is usual in the more primitive mammals (figs. 8 and 10), and that a more distal insertion (with or without the separation of this part as a distinct femorococcygeus) is a secondary modification in various orders of mammals. When M. tenuissimus is present, the courses of the nerve(s) to biceps ventrally to it, and of the nerves to Mm. glutaeus superficialis and femorococcygeus dorsally to it, are distinctive and assist

[1] Cf. also the otter (fig. 7).

in discriminating between these muscles. The localised attachment at or near a third trochanter (or corresponding ridge or depression) of the superficial glutaeal musculature has thus been found in Monotremata (the "glutaeus medius" of Westling), in the more primitive Marsupialia (*Dasyurus* and *Perameles*) and in various Xenarthra and Primates. The above-mentioned patellar or distal femoral attachment of femorococcygeus appears to have been formed by distalward extension of the insertion of the superficial glutaeal sheet (well illustrated among the Primates, fig. 10), and the subsequent specialisation of two distinct insertions, a good example of which is seen in the horse. Thus it is concluded that the primitive insertion of the superficial glutaeal musculature is in mammals just distal to that of the deeper glutaei on the great trochanter; a third trochanter, rudimentary in Monotremata, is differentiated at the site of its attachment. Romer (1922) has expressed a similar opinion, but he gave no consideration to the problem created by the existence in mammals of Mm. femorococcygeus and tenuissimus (*vide* pp. 405, 425).

The derivation of the superficial glutaeal as well as the deep glutaeal musculature from a common M. iliofemoralis is suggested by the innervation of part of the former by nerve bundles (N. glutaeus anterior) passing through the latter musculature, and the innervation of the deep glutaei by bundles of the same nerve. This is true of *Simia sat.*, *Hapale jacch.*, *Erethizon dors.* (fig. 15) and *Perameles obes.*, according to my own observations. It is widespread in mammals. Parsons indeed claimed the innervation of the whole of the superficial glutaeal musculature from N. glutaeus anterior (*seu* superior) in Rodentia, though in each of the rodents I have examined the posterior glutaeal nerve also supplies it (it seems clear that the hinder portion of this musculature was regarded by Parsons as "biceps," despite its innervation from N. glutaeus posterior). This innervation from N. glutaeus anterior, in addition to that from N. glutaeus posterior, is difficult to reconcile with the older views of Gadow and Leche as to the phylogeny of the superficial glutaeal musculature.

Further support for the conclusion reached in this paper is found in the attachment in some mammals of M. tensor fasciae latae to the third trochanter (e.g. *Tupaia*). Possibly the "gluteus ventralis" described by Parsons in Carnivora is a part of the same muscle, though it may be a direct derivative of the deep glutaei. Rodentia, e.g. *Lepus*, present a similar "glutaeus ventralis," in addition to a more distally-attached tensor fasciae latae.

Support for this view is also offered by Cunningham's observation of the continuity between the lateral margins of the superficial and deep glutaeal muscles in *Phalangista*. Further, the statement of Macalister (1873, p. 258) that certain Xenarthra possess a tensor fasciae latae innervated from N. femoralis and attached to the third trochanter, may prove to offer evidence in this direction. Should the nerve be found on renewed investigation to pass deep to M. rectus femoris, like the branch of N. femoralis which innervates part of the deep glutaeus ("glut. min."—Westling) of Monotremata, then support

would be given to the view deriving superficial and deep glutaeal musculature from a diploneural pro-mammalian iliofemoralis.

Osteological evidence is consistent with the view here advanced. The third trochanter is a neomorph in mammals, and appears to have been situated primitively about the middle of the lateral margin of the femur (as to-day in Monotremata (fig. 14), and various primitive Theria, e.g. some Xenarthra and Rodentia), and thus a little distal to the elongated great trochanter. Both of these trochanters may have been differentiated from the elongated "*glutaeal trochanter*" of the more mammal-like reptiles, the superficial part of M. iliofemoralis concentrating its attachment on the more distal part and remaining mainly abductor in function, while the deep part acquired a medial rotator and extensor function with the proximal enlargement of the great trochanter, and the pre-acetabular extension of the ilium.

Two objections to this view require to be met. The monotreme M. glutaeus superficialis is innervated solely from N. glutaeus posterior and there is no separate M. tensor fasciae latae. But it may be that the superficial delamination by which it was formed from M. iliofemoralis did not occur in precisely the same way as in Theria, and that no musculature innervated from Nn. glutaeus anterior or femoralis was included therein. It might also be argued that if femorococcygeus be not a representative of the reptilian extensor iliotibialis, then there is no distinct muscle in mammals corresponding to it. This objection is met in the discussion above regarding the phylogeny of the tenuissimus. This muscle perhaps comprises the whole of the metazonally-innervated superficial dorsal musculature. The pro-mammalian M. extensor iliotibialis may have been innervated solely from N. femoralis (as in some modern lizards); it is represented by M. rectus femoris in mammals.

It may be noted that Gregory and Camp concluded the femorococcygeus of the cat to be a survival of the reptilian "caudofemoralis," in consequence of the confusion which has existed in the use of this term. Parsons applied the name "caudofemoralis" (*seu* agitator caudae) to the M. femorococcygeus of Leche (1883) in many of his myological descriptions (e.g. Carnivora, 1897), though he recognised its community of nerve supply with M. glutaeus superficialis in Ungulata, and named it "femorococcygeus" (1903). Reighard and Jennings also applied the name "caudofemoralis" to M. femorococcygeus in the cat. Gregory and Camp (1918) converted this term into "caudifemoralis" and compared it with Gadow's "caudifemoralis" of reptiles. The latter is, however, a muscle of totally distinct phylogenetic history (p. 409), and is the muscle named "femorocaudalis" by Frets in *Sphenodon*; it is shown in this paper to be represented in mammals, not by the femorococcygeus of Leche, but by the muscle he named "caudofemoralis" in Menotyphla. Forster (1918) has added to the confusion by erroneously describing M. flexor cruris caput dorsale (*mihi*) in various mammals as a M. "caudofemoralis," and by regarding it as a derivative of the glutaeal musculature.

Confusion of terms has arisen in another direction from varied usage of the term "agitator caudae." By Humphry it was employed (1872, p. 158)

synonymously with the term "caudofemoralis" in the same sense as that in which Leche later employed the latter term. But by Macalister "agitator caudae" was the name extensively employed (e.g. 1878, p. 268), in the meaning of Leche's "femorococcygeus" (cf. p. 413 *infra*); Parsons frequently used it in Macalister's sense of the word. On the other hand, the "caudal head of biceps" was the name used by both Parsons (1894 and 1896) and Macalister (1878, p. 290) for the femorococcygeus (Leche) of Rodentia.

### 3. M. PYRIFORMIS

Leche pointed out that M. pyriformis is in *Tupaia* dorsal to N. ischiadicus. This is also true of *Lepus*, *Lutra* and other Eutheria in which I have ascertained its presence (excepting the occasional passage through it in Man of N. peronaeus). It appears to have been differentiated independently in various orders, viz. in Primates, Rodentia, Carnivora and Insectivora. Thus the pyriformis of Man (Hepburn, 1892), and of certain Carnivora (Parsons) and Insectivora (Leche), has been formed within the orders concerned from the glutaeus medius. Parsons' observations on Rodentia point to its formation independently in various families (1894, p. 284), viz. in *Sphingurus*, Octodontidae and most Sciuromorpha; in these it was formed from M. glutaeus minimus. In Dasyproctidae, on the other hand, it appears to have been formed from M. glutaeus medius.

The innervation, where known, is consistent with these views, for the nerve is more closely associated with the glutaeal nerves and N. peronaeus than with ventral nerves, such as Nn. ischiadicus ventralis and tibialis. Gadow's suggested derivation (1882) of the human pyriformis from a reptilian "caudi-ilio-femoralis" (Gadow), which has been adopted by many writers (e.g. Romer, 1922; Pearson, 1926), cannot be retained in view of the above observations and of the evidence here presented that the mammalian M. caudofemoralis represents both this reptilian muscle and Gadow's caudifemoralis.

Most writers on Marsupialia and Monotremata have described M. caudofemoralis as a "pyriformis," evidently on account of the similarity of its position to the pyriformis found among Eutheria. It presents, however, very different relations to nerve trunks (figs. 11 and 14). No true pyriformis has yet been described in non-eutherian mammals. Gregory and Camp (1918, p. 498) compared the mammalian pyriformis with a part of the femorocaudalis (Frets' rhynchocephalian term) of crocodiles and lizards, citing the close association of the nerve to the pyriformis with the peronaeal and tibial nerves; but this may be claimed with equal truth for any metazonal nerve and is useless as evidence for their view. M. pyriformis appears to be a neomorph among Eutheria.

### 4. M. CAUDOFEMORALIS

The comparison of thigh structures already made points to the following muscles being phylogenetic equivalents: caudalifemoralis[1] (de Man) in Urodela,

[1] It is to be observed (cf. p. 371) that the caudalifemoralis (like certain other muscles in Urodela, p. 375) presents individual variations in its relations to large nerve-trunks (e.g. *Crypto-*

pyriformis (Gaupp) in Salientia, femorocaudalis (Frets) in *Sphenodon*, caudi-ilio-femoralis (Gadow) in Chelonia and Aves, both caudi-ilio-femoralis and caudi-femoralis (Gadow) in Crocodilia[1] and Lacertilia, caudofemoralis (Leche) in Eutheria, pyriformis (Meckel, Mivart and Pearson) in *Ornithorhynchus*, caudofemoralis (Westling) in *Echidna*, and pyriformis (Macalister, Parsons and Frets) in Marsupialia (cf. fig. 11). To all these muscles it is claimed that Leche's term, M. caudofemoralis (1883, p. 90), may be appropriately applied. The caudocrural muscle (Humphry)—the caudalipuboischiotibialis (de Man) (fig. 2 *supra*), found in Urodela and rarely in Salientia (Noble, 1922, p. 33), was probably derived from the same primitive caudofemoral musculature as the caudalifemoralis of Urodela (cf. p. 419). Bland Sutton has compared it with the part of the reptilian caudofemoralis distinguished by Gadow in Crocodilia and Lacertilia as "caudi-femoralis," on the ground that the long tendon of the latter (extending to the fibula, cf. fig. 3) might be compared with the ischio-flexorius (de Man) of urodeles (to which the caudocrural is attached). Humphry compared it with the caudal head of the mammalian semitendinosus. Gadow compared it with his "flexor tibialis externus" (1882, p. 402). There are difficulties in the way of all these views (pp. 419, 421).

There is indeed no ground for the assumption that the caudocrural is necessarily represented by any separate muscle in Amniota, for it has completely disappeared in most Salientia (Noble), and there is evidence (p. 427) that modern urodeles as well as frogs have undergone considerable specialisation of the hind limb since their divergence from the forerunners of modern Amniota.

The muscles thus homologised throughout Tetrapoda are found to justify by their attachments, general relations and innervation, the identification based on relations to main nerve trunks. Special interest attaches to those groups (frogs, birds and mammals) in which the great caudofemoral retractor musculature of more primitive Tetrapoda has been almost completely replaced by a new apparatus for limb retraction, viz. by the iliofemoralis (glutaeal) and flexor cruris (hamstring) musculature (fig. 9). In these groups it is significant of the morphological conservatism of the thigh structures that slender muscles are still found which, despite their small size, present the characteristic features of the large caudofemoral retractor; they are entitled to be regarded as the vestiges of this former important muscle mass. Transference of the origin in some birds and mammals (fig. 5) to the tuber ischii is no objection to the suggested homology. Nor again does the close association of the nerve-supply in Eutheria and birds with N. ischiadicus ventralis constitute a difficulty; for it still follows essentially the same course

*branchus jap.* Humphry, 1872, p. 53). In *Cryptobranchus allegh.* N. tibialis may encircle this muscle (cf. Low, *P.Z.S.* 1926, p. 928) or it may pass dorsally to it (fig. 1 *supra*).

[1] Romer (1923, pp. 539, 544) has pointed out an error in Gadow's text in which he described a part of the iliofemoralis as "caudi-ilio-femoralis" and a caudi-ilio-femoralis (similar to that of other reptiles) as "caudi-femoralis Theil 2" (1882, p. 392). Gadow's figure 34, on the other hand, shows all these muscles correctly named.

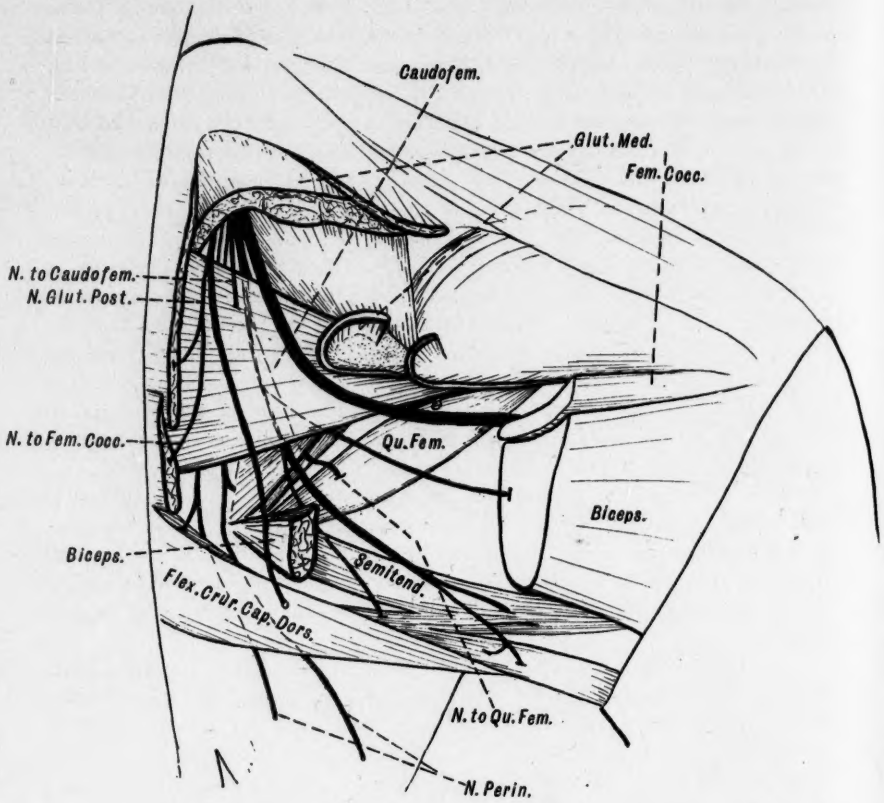


Fig. 11. *Perameles obesula.* Right thigh and glutaeal region, × 1½. Position and dissection similar to that of *Talpa* in fig. 6. A considerable part of M. glutaeus medius has also been removed. M. caudofemoralis has a situation similar to that of the M. pyriformis of various Eutheria. Its relations are however totally different, and it presents the characteristic features of M. caudofemoralis present in many other mammals, as in other Tetrapoda. It intervenes between Nn. tibialis et peronaeus and N. ischiadicus ventralis ("nerve to the hamstrings"—Cunningham). N. cutaneus femoris posterior passes dorsally to it, as also the nerves to Mm. glutaeus superficialis and femorococcygeus, derivatives of M. iliofemoralis. The N. ischiadicus ventralis forms a single trunk (apart from the nerve bundle supplying the dorsal head of M. flexor cruris); in this respect Marsupialia resemble Monotremata and differ from Eutheria which have a "nerve to quadratus femoris" distinct usually from the nerves to the hamstring muscles. The nerve to quadratus femoris is continued into a more distally-inserted part of M. quadratus femoris, described by Cunningham as "a part of adductor magnus" (cf. fig. 10 D). The mode of union of the various parts of M. flexor cruris has not attained the condition characteristic of most Eutheria (p. 423).

as in urodeles and reptiles, though displaced further into the thigh owing to M. caudofemoralis having become almost entirely a thigh muscle. In mammals the insertion (fig. 12) differs considerably in the three sub-classes, being proximal in Marsupialia (the so-called "pyriformis") (fig. 11), and generally near the distal end of the femur in Eutheria, while in Monotremata it is near the middle of the femur (figs. 12 and 14). These may, however, be interpreted as related to divergent modification of function subsequent to the abrogation of the former retractor function, being abductor like a pyriformis in Marsupialia and hip-extensor like a hamstring in Eutheria.

In birds and Urodela (fig. 12), and apparently in Rhachitomi, Cotylosauria[1] and in various Dinosauria, it is more distally situated (viz. near the middle of the shaft) than in modern reptiles or the frogs, in which the insertion has moved to the proximal end of the femur (perhaps in relation to a relative elongation of the femur itself). These differences provide no serious obstacle to the identifications proposed.

Further support for the homology of the mammalian muscles with the caudofemoral retractor of reptiles is offered by the distribution of M. caudofemoralis in mammals; for it occurs in the more primitive of them. I have found it *present* (figs. 4–9, 11, 14, 15) in *Ornithorhynchus* and *Echidna*, in *Manis*, in *Tatusia peba*, *Tupaia pict.*[2], *Macroscelides* sp.[2], *Talpa eur.*, *Erinaceus eur.*, *Erethizon dors.*, *Cavia porc.*, *Mus dec.*, *Pteropus med.*, *Lemur lem.*, *Tarsius spectr.*, *Galago crass.*, *Hapale jacch.*, *Lutra vulg.* and *Genetta vulg.*; in *Perameles obes.* and *Dasyurus mac.* Published accounts point to its presence in most marsupials, many rodents, and perhaps all Insectivora. I find it *absent* in *Lepus cun.*, various catarrhine monkeys, apes and Man, *Perodicticus potto*, *Loris grac.* and *Nycticebus tard.*, *Ateles* sp.; in *Canis vulg.*, *Felis cat.*, *Meles tax.*, *Ursus him.*, *Ovis ov.*, *Bos taur.* and *Sus*; in *Equus cab.* and *Hyrax cap.* It appears from Parsons' descriptions to be absent in all Artiodactyla.

Extensive re-investigation of the Mammalia will be necessary to determine its complete distribution, for it is rare to find recorded the detailed course of the nerves to Mm. biceps, semitendinosus and semimembranosus; and definite distinction of M. caudofemoralis from hamstring musculature requires knowledge on this point (p. 394). Thus it appears that M. caudofemoralis has in Eutheria been frequently regarded as a part of semimembranosus (Parsons in Rodentia, Leche in Lipotyphla and the cat), while Carlsson has described a muscle by this name in *Hypsiprymnodon*, which may prove on examination to be some derivative of quadratus femoris (cf. p. 426). The confusion, to which reference has been made above (p. 407), attaching to the use of the term "caudofemoralis," seems to be traceable mainly to the use of the name "agitator caudae" for a true M. caudofemoralis (Leche) by Humphry but by Macalister for a M. femorococcygeus (Leche).

[1] Cf. the femur of the Pelycosaur *Dimetrodon* figured on p. 412 (fig. 12).

[2] *Vide* footnote 3 on p. 384, regarding other Menotyphla.

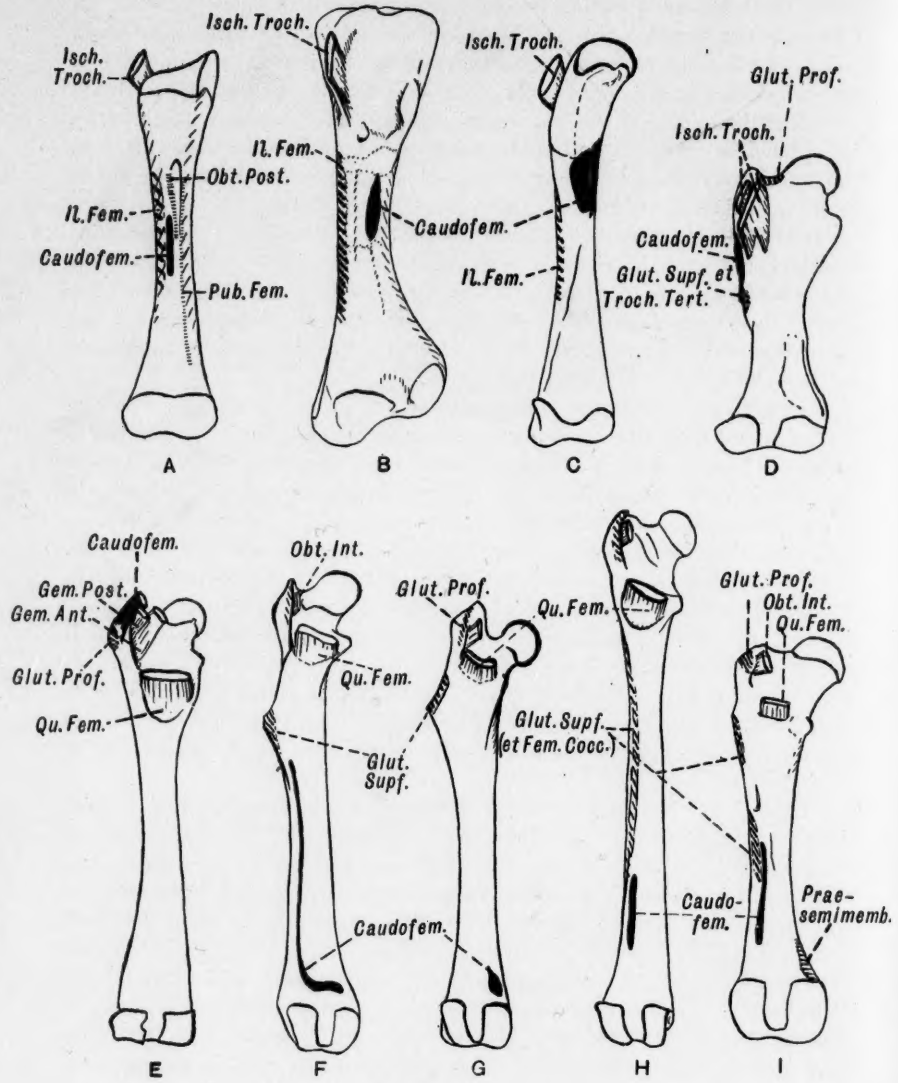


Fig. 12. For description see p. 413.

Fig. 12. A. *Salamandra mac.* × 6, B. *Dimetrodon* sp. × ⅓, C. *Crocodilus nil.* × ⅜, D. *Echidna acul.* × 1, E. *Dasyurus mac.* × ¾, F. *Tupaia pict.* × ⅝, G. *Macroscelides* × 3, H. *Hapale jacch.* × 1½, I. *Lutra vulg.* × ⅝. Femora, ventral views, showing sites of attachment of Mm. obturator posterior (p. 374), iliofemoralis (p. 406), ischiotrochantericus (p. 426), and caudofemoralis (p. 409).

The insertion of M. caudofemoralis, which is near the middle of the femur in the more primitive Tetrapoda, has become displaced towards the lateral margin in *Ornithorhynchus* and to the margin itself in *Echidna*. In Marsupialia it has been displaced proximally to the great trochanter (a less extreme instance than *Dasyurus* being shown in fig. 11), while in Eutheria the insertion has moved distally, being generally restricted to the shaft near the origin of M. gastrocnemius.

M. ischiotrochantericus has become differentiated in most mammals (though not in Monotremata), into Mm. obturator internus and quadratus femoris, the insertion of the latter extending more distally in most Marsupialia (cf. fig. 11) than in *Dasyurus*.

In Lacertilia and Urodela it would appear that the plane of cleavage in the deep ventral musculature has not occurred in the same way as in many groups (if innervation is reliable as a guide); for the metazonally-innervated part comprises not only a M. ischiotrochantericus but also a M. obturator posterior. M. iliofemoralis, attached to the ventro-lateral part of the shaft in primitive Tetrapoda, has acquired two distinct insertions in all mammals (fig. 12 D), with associated differentiation of the Therapsid "glutaeal trochanter" into the "third" and "great trochanters." Secondary extension of the former insertion along the femur occurs in many Theria (figs. 12 H and I).

Many Urodela (p. 428) have become specialised in the differentiation of a M. pubifemoralis from an overlying hamstring muscle (M. pubotibialis, de Man). Many Therian mammals show a similar extension of M. semimembranosus on to the femur, with differentiation of a M. praesemimembranosus (fig. 12 I).

In Urodela the deep flexor musculature comprises a M. ischiotrochantericus and a M. obturator posterior (p. 414).

Thus Parsons employed the name "caudofemoralis" as synonymous with "agitator caudae" for M. femorococcygeus, and therefore in a different sense to Leche (Menotyphla) who used it in Humphry's meaning. Forster has applied the term "caudofemoralis" to M. flexor cruris caput dorsale, consequent on his erroneous identification of this muscle in Monotremata (pp. 407, 420) as glutaeal musculature and the usage of this term by Parsons.

Most writers on Monotremata and Marsupialia (*vide* figs. 11, 12 and 14) have described M. caudofemoralis as a "pyriformis," thus implying its homology with the muscle so named in Man and other Eutheria. Leche and Westling have, on the other hand, recognised its homology with M. caudofemoralis (Leche) of Eutheria. Its identification as a "pyriformis" ignores the existence in many Eutheria and in most other Tetrapoda of a M. caudofemoralis, agreeing in every essential feature with the monotreme and marsupial muscle in question. It also involves our disregarding the extensive differences between M. pyriformis of Eutheria and the supposed "pyriformis" of other mammals. The latter is between Nn. tibialis et cutaneus femoris posterior and Nn. ischiadicus ventralis et perinaealis, and its nerve supply is associated with the tibial and ventral sciatic nerves (features characteristic of M. caudofemoralis throughout Tetrapoda); the eutherian pyriformis is, on the other hand, dorsal to Nn. peronaeus, tibialis, cutaneus femoris posterior, and ischiadicus ventralis, and it is innervated in association with Nn. peronaeus and glutaei.

We should have to revise our conclusion (p. 408 *supra*) that M. pyriformis is a neomorph derived in various eutherian orders from the deep glutaeal muscles and it would be necessary to regard the supposed absence of a M. caudofemoralis in Monotremata and Marsupialia as a secondary modification rarely found in the more primitive Eutheria.

The identification, then, of this muscle in Marsupialia and Monotremata with the eutherian M. pyriformis, is contrary to the evidence which is available, and it is dismissed as wholly improbable despite Frets' plea to the contrary (1909, p. 93).

Gregory and Camp have failed in their review of mammalian myology (1918) to realise the homology of Westling's "caudofemoralis" in *Echidna* with the so-called "pyriformis" of various descriptions of *Ornithorhynchus*.

Romer (1922) and Pearson (1926) have omitted consideration of the existence in mammals of a "caudofemoralis" (described by Leche in Insectivora and by Westling in *Echidna*).

### 5. Musculature innervated from N. ischiadicus ventralis

#### (*a*) *Reptilia and Urodela*

A comparison of the distribution of N. ischiadicus ventralis in these groups reveals two conspicuous differences in its distribution (pp. 371, 373, 381, 409), viz. (1) its innervation in reptiles of superficial musculature passing from a dorsal origin (on ilium and vertebral column) to the shank, i.e. M. flexor cruris caput dorsale, and (2) its innervation in Urodela of superficial ventral musculature passing from a pubic origin to the shank, i.e. M. pubotibialis (de Man). The remainder of N. ischiadicus ventralis has a similar distribution in the two groups, viz. to the superficial and deep musculature taking origin from the ischium, of which the former is M. flexor cruris caput ventrale (perhaps wanting in Chelonia, cf. Ogushi, 1913). Variations in the connections of the ventral with the dorsal head of M. flexor cruris are considered below.

The deep musculature, conveniently distinguished as M. flexor profundus, comprises in all reptiles a short muscle (Osawa's "ischiotrochantericus") (fig. 12), resembling the ischiofemoralis (de Man) of Urodela. In Lacertilia and Chelonia, as in Urodela (figs. 1, 12), there is also a M. obturator posterior (M. pubi-ischio-femoralis externus, *partim*, Gadow) attached to the internal trochanter and partly continuous rostrally with a similar muscle of obturator innervation. In Lacertilia there is still another deep muscle which is inserted on the adductor line (M. ischiofemoralis, Gadow). Gadow has described a similar muscle in Crocodilia (pubi-ischio-femoralis posterior, Hauptheil), but this is innervated (in my specimens of alligator and crocodile) only by N. obturator (confirmed by study of serial sections of *Alligator miss.* embryo). Romer has described its innervation in *Alligator miss.* from both the obturator and sciatic nerves (1923, p. 542).

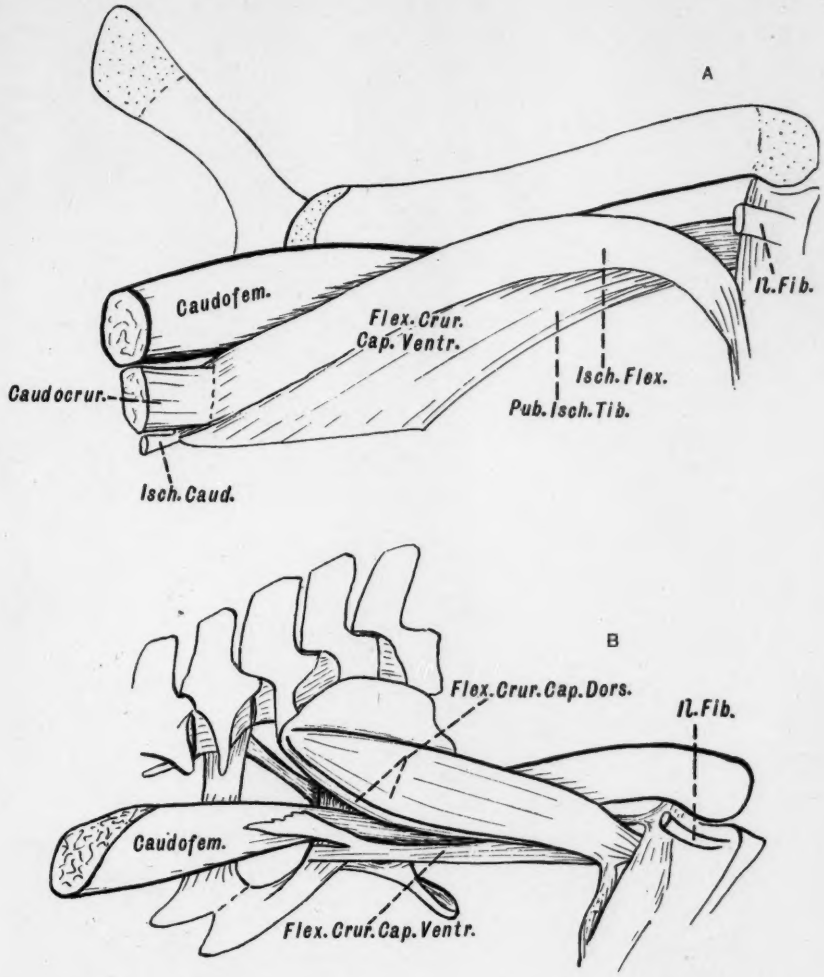


Fig. 13. A. *Salamandra mac.* × 6., B. *Alligator miss.* × $\frac{2}{3}$: caudal views of right thighs, showing the difference between the M. flexor cruris of Amniota and that of Amphibia. In the Amniota this muscle takes origin by a ventral head, ventrally to M. caudofemoralis, and by a dorsal head dorsally to this muscle. In Lacertilia and *Sphenodon* the dorsal head of origin is attached mainly to the vertebral column (fig. 14 A); this is also the case in those mammals which retain it (figs. 4, 6, 7, 8, 11, 14 B and 15). In Amphibia the dorsal head of origin is wanting. In Amniota it is innervated by a recurrent branch of N. ischiadicus ventralis (cf. fig. 9). An intermediate slip between the ventral and dorsal heads is present in Crocodilia, attached to the fascia covering M. caudofemoralis (*vide* p. 419).

The differences in distribution of N. ischiadicus ventralis, to which attention has been drawn, constitute no objection to the homologisation of N. ischiadicus ventralis in the various groups, which has been made on the basis of its course relative to bone and musculature (pp. 396, 409). Evidence is indeed found that phylogenetic muscular changes are responsible, in part at least, for the observed differences of distribution.

The respective spheres of innervation of diazonal nerves and metazonal nerves differ in fish from those in urodeles[1]. I have traced no data relating to fish which indicate the overlapping of diazonally-innervated musculature by a metazonally-innervated superficial ventral sheet such as we find in urodeles. In *Acanthias*, *Chimaera* and *Acipenser* metazonally-innervated musculature appears from Davidoff's account (1879, pp. 465, 482, figs. 17 and 32) to be on the post-axial side of that supplied by diazonal nerves. In *Chimaera*, moreover, the latter nerves supply the pre-axial part of the superficial sheet. A modification of some kind has occurred in urodeles, whether we postulate encroachment on diazonal territory by metazonal nerves, or whether, as is more probable, we suppose a phylogenetic extension of the more post-axial musculature as an adaptive modification. The extent of overlap is variable among urodeles (Mivart). The difference in the distribution of N. ischiadicus ventralis in urodeles and reptiles in respect of the superficial ventral sheet thus appears attributable to specialisation of the Urodela (*vide* also p. 427).

The musculature I describe as the dorsal head of M. flexor cruris in reptiles (and other Amniota) is unlike any urodele muscle. Inasmuch as it has been in many instances mistaken for other muscles in Amniota some revision of existing accounts becomes necessary.

Gadow's account of the Lacertilian M. flexor tibialis externus requires amendment. He describes it as ending proximally in the ilio-ischiadic ligament, with an attachment to the ilium in some lizards. This description makes the lizards appear to differ considerably from *Sphenodon*, according to Gadow's own account, for in the latter this muscle is attached to caudal vertebrae, dorsally to M. caudifemoralis. The description of *Sphenodon* is corroborated by Frets (1909, fig. 4 I), who figures the innervation of this caudally-attached musculature by a twig from the nerve supplying the thigh portion of the muscle.

Examination of various Lacertilia has satisfied me that the lizards as well as *Sphenodon* possess a caudally-attached "flexor tibialis externus" (Gadow), viz. a *M. flexor cruris caput dorsale*. In *Lacerta vir.*, *Uromastix spin.* and *Varanus beng.* the twig which supplies the part of the muscle on the caudal side of the semi-intersection generally known as the ilio-ischiadic ligament leaves the nerve supplying the thigh portion of the muscle close to the intersection, and passes across its deep aspect. The intersection is incomplete in each of them; the musculature is continuous across its deep aspect, and Gadow has indeed described it as a half-fleshy tendon in *Sphenodon* (1882,

[1] The respective spheres of innervation of these nerves have also been discussed, pp. 381, 422, 429.

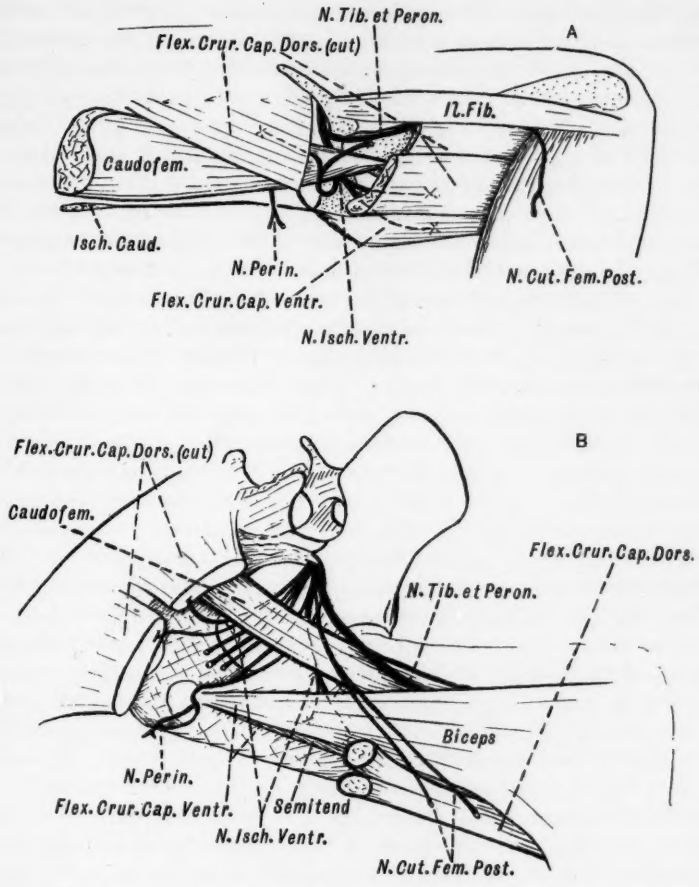


Fig. 14. A. *Lacerta vir.* × 2, B. *Echidna acul.* × $\frac{2}{3}$. Caudal views of right thighs and post-axial groins. The caudally-attached dorsal head of M. flexor cruris is innervated by a recurrent branch of N. ischiadicus ventralis in Lacertilia like the dorsal head of that muscle in other Reptilia (fig. 13 B). The nerve to the more caudal part of this head passes across the deep surface of the tendinous semitendinous intersection found in M. flexor cruris caput dorsale of Lacertilia and *Sphenodon* in the region of the "post-axial groin." In Monotremata (p. 420) the dorsal head of flexor cruris is greatly enlarged and from it cutaneous musculature appears to have been delaminated. It is innervated by branches of N. ischiadicus ventralis which first pass ventrally to M. caudofemoralis, as in Amniota generally. The monotreme M. caudofemoralis presents relations like those of the great caudofemoral retractor of Reptilia and Amphibia (figs. 1, 3 and 13), and quite unlike those of the eutherian "pyriformis"; it is between N. tibialis and N. cutaneus femoris posterior on its dorsal aspect and N. ischiadicus ventralis and N. perinaealis on its ventral aspect (cf. p. 394).

p. 396). Osawa and Perrin regarded the caudally-attached part of the muscle in *Sphenodon* as a part of the caudofemoral musculature, but Frets correctly reverted to Gadow's earlier interpretation on the evidence of the nerve-supply, which is unassociated with that of M. caudofemoralis (femorocaudalis Frets). The semi-intersection or "ilio-ischiadic ligament" of various authors appears to be related to the sharp angle existing at the "post-axial groin" between the caudal and thigh portions of this flexor musculature. It is found only in *Sphenodon* and Lacertilia, and in these only is there a sharp angle in the musculature. In Crocodilia and Chelonia, in which there is no intersection, there is again a dorsal head of M. flexor cruris; but it is attached to the ilium and passes directly to its shank insertion without having to turn round the "post-axial groin." This interpretation of the ilio-ischiadic ligament as a neomorph arising within the flexor cruris musculature is supported by the observation that the intersection is restricted to the superficial part of the musculature.

Humphry suggested a comparison of this intersection with that found in Urodela where the caudocrural joins the ischioflexorius (de Man), and with that frequently found in the semitendinosus of mammals (p. 421 *infra*). Thus he was led to the inference that the intersection ("ilio-ischiadic ligament") of reptiles separates two distinct muscles, of which the more caudal represents the urodele caudocrural. The evidence which has been considered above points, however, directly against Humphry's account of the phylogeny of the caudocrural muscle and "ilio-ischiadic ligament." The connection of this ligament with the ilium appears to be secondary.

Romer has repeated errors of Osawa, Gadow, Bland Sutton and Humphry in his recent study of the caudofemoral musculature in mammalian phylogeny (1922, p. 572). Osawa's coccygeo-femoralis brevis of *Sphenodon* (clearly shown by Frets to be a part of the flexor musculature) is accepted as equivalent to Gadow's caudi-ilio-femoralis (in other reptiles), which is in turn erroneously compared with the mammalian pyriformis, following Gadow. He has adopted Bland Sutton's comparison of the urodele caudocrural with the reptilian caudi-femoralis of Gadow, and has combined with it Humphry's comparison of the former with the caudal head of the mammalian semitendinosus (p. 421 *infra*). Thus it is that the coccygeo-femoralis longus (i.e. femorocaudalis Frets) is compared with the caudal slips which join mammalian hamstrings, whereas these are shown by Frets (1909) and the present writer to be homologous with the so-called "coccygeo-femoralis brevis" of *Sphenodon*. Romer's suggested comparison of the reptilian ilio-ischiadic ligament with the sacro-ischiadic ligament of mammals (1922, p. 561) is untenable, in view of the distribution of these ligaments in the two classes and of their relations to muscles and nerves, a subject which will be reserved for a paper I hope to publish shortly.

The suggestions of both Bland Sutton and Humphry meet with difficulties. Bland Sutton found in his comparison a means of accounting for the long tendon attached to the caudofemoral musculature as a retrogressed vestige

of the flexor musculature to which the caudocrural is attached. It must, however, be observed that (1) Mm. caudi-femoralis and caudi-iliofemoralis of Lacertilia and Crocodilia have not improbably differentiated within the reptilian class from a common mass resembling M. femorocaudalis (Frets) of *Sphenodon*, as Gadow indeed himself recognised; (2) the caudocrural has been lost without leaving a trace in most Salientia, and thus, even if it had been present in reptilian forerunners, no representative would necessarily be retained; (3) the pelvic and femoral attachments of the caudocrural and ischioflexorius are unlike those of the reptilian caudifemoralis and its long tendon; and (4) the long tendon of the reptilian caudifemoralis is wanting in Chelonia, according to Gadow's descriptions, and is unknown in mammals and birds. In default of direct evidence in favour of Bland Sutton's hypothesis it must be concluded that the long tendon of the reptilian caudifemoralis is probably not a remnant of the urodele ischioflexorius. It may be a reptilian neomorph, though it possibly represents a former distally-attached part of the caudofemoral musculature differentiated from the remainder in a manner like that postulated (though perhaps incorrectly, p. 426) by Gadow for the caud-ilio-flexorius of birds (1891, p. 163). The varying relations of the tendon to nerve trunks (Gadow, 1882, p. 352) perhaps point to its being a neomorph. New aponeurotic connections not infrequently make their appearance in phylogeny, e.g. that of tensor fasciae latae in many mammals.

All modern reptiles, then, are distinguished from amphibia in the possession of a dorsal head of origin by M. flexor cruris. Its relations and mode of innervation are consistent with the hypothesis that it has been formed by dorsal extension round the lateral surface of M. caudofemoralis from the primitive ischial attachment, to caudal vertebrae in Lacertilia and *Sphenodon*, to ilium in Chelonia and Crocodilia, and that the nerve supply has acquired its somewhat recurrent course by following the musculature in its migration.

Two alternative hypotheses require consideration. It might be claimed that the common attachment to caudal vertebrae of M. flexor cruris caput dorsale and of M. caudofemoralis (retained in *Sphenodon* and Lacertilia) is a primitive tetrapod arrangement, the muscles having perhaps become distinct through differentiation of their sites of insertion. But this interpretation fails to offer an account of the recurrent course of the nerve-supply of the former muscle. There are serious objections to another view which would account for this recurrent nerve-supply by supposing the muscle to have been formed by dorsal migration of the origin of a urodele-like caudocrural, viz. (1) there is no intersection in Crocodilia, Chelonia, Aves or the more primitive Mammalia (p. 421) comparable with that associated with the caudocrural of Urodela, and (2) the nerve-supplies of the urodele caudocrural and flexor cruris are derived from different nerves, viz. Nn. pudendus and ischiadicus ventralis respectively, but the whole of the dorsal head of the flexor cruris in reptiles is innervated from the same nerve as the ventral head, viz. N. ischiadicus ventralis (and even from the same branch of that

nerve in the Lacertilia despite the intervention of a semi-intersection between the caudal and thigh portions of the muscle, fig. 14 A).

It is concluded that the reptilian dorsal head is a caenotelic feature of the flexor cruris, and that it has been retained in a modified form (fig. 9 and p. 421) in birds and mammals.

The insertion of M. flexor cruris is similar in urodeles and reptiles, the principal difference consisting in the differentiation of a lateral insertion in reptiles between the two heads of gastrocnemius. The dorsal and ventral heads of M. flexor cruris remain distinct to their insertion in most reptiles, the dorsal head appropriating the lateral insertion and the attachment on M. gastrocnemius.

The ventral and dorsal heads of M. flexor cruris have been given various names in reptiles. In addition to those set out in the table of synonyms (p. 434), the following may be noted:

| | | Caput ventrale | Caput dorsale |
|---|---|---|---|
| Rhynchocephalia | Gadow | Flexor tibialis internus | Flexor tibialis externus |
| | Osawa | Ischiotibialis posterior | Coccygeo-femoralis brevis |
| Chelonia | Gadow | Wanting | Flexor tibialis externus (pars iliaca) et flexor tibialis internus (pars caudalis) |

### (*b*) *Mammalia, Aves and Salientia*

In mammals both the dorsal and ventral heads of M. flexor cruris, already described in reptiles, are readily distinguishable, though the phylogeny of the dorsal head has been generally misunderstood. The homology of the large buttock muscle of Monotremata (fig. 14 B), generally described as "glutaeus maximus" (e.g. Westling, 1890), with the dorsal head of the reptilian M. flexor cruris, has been overlooked. Frets indeed realised the significance of the "caudal head of biceps" described by Macalister and Cunningham in marsupials for the interpretation of the caudal head of his "M. flexor cruris profundus" in *Sphenodon* (1909, p. 95); but he mistook the monotreme muscle, like other writers. On the other hand, Forster (1918, pp. 150, 164) and Pearson (1926, p. 153) have noted the resemblance of this monotreme muscle to the "caudal head of semitendinosus" in *Lepus* and to the "crurococcygeus" (Coues) in *Didelphys* respectively. Each, however, fell into error; for the former argued that the therian muscles must be glutaeal in character (using Macalister's term "caudofemoralis"), while the latter repeated Romer's error in supposing these mammalian muscles to represent the coccygeo-femoralis longus (of *Sphenodon*) and the urodele caudocrural.

Westling's "glutaeus maximus" in Monotremata (fig. 14 B) presents every characteristic feature of the reptilian M. flexor cruris caput dorsale, as well as of the muscle described by this name (figs. 4 and 6) in Insectivora (Leche's caudal head of semitendinosus). Its origin is dorsal to that of M. caudofemoralis (pyriformis Frets), and dorsal also to that of M. glut. superficialis

("glut. medius" Westling). N. perinaealis and N. pudendus pass ventrally to it, between it and M. flexor cruris cap. ventr. (of which "biceps" forms a part). N. cutaneus femoris posterior reaches the surface at its rostro-dorsal margin. It is supplied by branches of N. ischiadicus ventralis which reach it by a recurrent course ventrally and round the distal margin of M. caudofemoralis (this nerve was erroneously described as "N. glutaeus inferior" by Westling and Frets in consequence of their identification of the muscle as "glutaeus maximus"). This muscle differs completely from the glutaeus maximus (*seu* superficialis) of Theria in its attachments (p. 405), its relations to adjacent muscles, its relations to cutaneous nerves (p. 399), and in its mode of innervation. Whereas its nerve passes ventrally to M. caudofemoralis (Leche), the N. glutaeus posterior of Monotremata and other mammals passes dorsally to it (p. 398 and fig. 15). The large size of the monotreme M. flexor cruris cap. dors. appears to have been responsible for its very general identification as glutaeal musculature.

In Theria M. flexor cruris cap. dors. is generally represented by a small caudal slip joining the main hamstring muscle mass. It has been variously named "the caudal head of semitendinosus" (Leche) or "of biceps" (Macalister and Cunningham). Of previous writers, Frets (1909) alone has realised its close phylogenetic connection with the dorsal head of the reptilian flexor cruris; most have followed Humphry in deriving it from the urodele caudocrural (which was in turn compared by Bland Sutton with the reptilian caudi-femoralis, p. 418 *supra*). The muscle is seldom large (it was found relatively extensive in *Erethizon dors.*, fig. 15) and it is often wanting.

Humphry based his claim mainly on the presence of a *tendinous intersection* in the mammalian semitendinosus, which he compared with the intersection related to the urodele caudocrural. Difficulties beset this hypothesis as follows: (1) the intersection is absent in birds and reptiles (the ilio-ischiadic ligament supposed to represent it in certain reptiles is a reptilian neomorph, p. 418); (2) there is no evidence of the presence or retention in reptiles of any separate representative of the caudocrural (p. 419); (3) the intersection is absent in some mammals, including some of the more primitive, viz. *Cyclothurus* and *Manis* (Humphry), Edentata (possibly a trace in *Chlamydophorus*—Macalister), Marsupialia (Macalister), *Thylacinus* (a faint one—Cunningham), *Phalangista* (Cunningham), Monotremata and *Erethizon*; (4) the caudal head of biceps, which replaces that of semitendinosus in *Erethizon* and certain Marsupialia (possibly also in certain Carnivora according to Cuvier's descriptions), presents no tendinous intersection so far as is known; (5) the caudal head of semitendinosus (or biceps) presents features which definitely identify it with M. flexor cruris caput dorsale, already described in reptiles and Monotremata, viz. its relations to cutaneous nerves and adjacent muscles, and its innervation through N. ischiadicus ventralis, the nerve bundle passing ventrally to both Mm. tenuissimus and caudofemoralis Leche.

It thus appears that the intersection is a mammalian neomorph, a conclusion also reached by Forster. This author, however, misunderstood the

character of the caudal hamstring head, as already pointed out; he supposed it to be glutaeal musculature.

The distribution of M. flexor cruris caput dorsale in mammals is consistent with the account here given of its phylogeny; like M. caudofemoralis, it is a survival of similar musculature in pro-mammalian reptiles. It is present in Dasyuridae (Leche), *Dasyurus mac.*, *Perameles obes.*, *Didelphys virg.* (Coues and Cuvier), *Thylacinus* and *Phalangista* (Cunningham), *Bettongia* (Cuvier), but absent in various Macropodinae (Macalister, Parsons, Frets). It is present in Insectivora generally, except in *Macroscelides*[1] and *Erinaceus* (Leche). Among Carnivora it is present in various Procyonidae, most Mustelidae and Viverridae, but absent in Canidae, Ursidae, Felidae and Hyaenidae (Parsons). I find it wanting in the dog and cat, Himalayan bear and *Meles tax.*, present in *Lutra vulg.* and *Genetta vulg.* Parsons' descriptions of Rodentia suggest its widespread occurrence. I find it in the mouse, rat, guinea-pig, rabbit and in *Erethizon dors.* I find it present in *Hapale jacch.* and Leche found it in *Cheiromys*, otherwise it appears to be absent in Primates. Macalister's descriptions show its presence in Xenarthra and in *Manis*. It has been retained in the horse and tapir (Parsons, 1903), and it is found in the pig and a very few other Artiodactyla. It is present in *Hyrax cap.*, where it forms a caudal head for M. semitendinosus.

*Attachments of M. flexor cruris*

(i) *Mammalia.* The caudal (i.e. the dorsal) head of origin has in mammals an orientation to thigh structures similar to that of the iliac head in Crocodilia (fig. 13) and Chelonia. The ventral head arises from the ischium as in reptiles. Mammals show noteworthy differences from reptiles in the mode of connection of the heads of origin with the respective distal attachments, and in the attachment of a part of the musculature (M. biceps cruris, p. 424) on the lateral side of *both* heads of gastrocnemius.

In most mammals the lateral insertion belongs to musculature with an ischial origin (M. flexor cruris cap. ventr.), while the medial insertion belongs to both ventral and dorsal heads of origin. The ventral head thus comprises M. *biceps*, and Mm. *semitendinosus* and *semimembranosus* (part of which is sometimes differentiated as a *praesemimembranosus*, e.g. Carnivora and Primates), though rarely (*Erethizon dors.*, fig. 15) the two latter are not distinct. In reptiles the cleavage of M. flexor cruris is different, for the more lateral insertion belongs to the dorsal head while the medial one belongs mainly or entirely to the ventral head, except in Chelonia which appear to possess no ventral head (adductor musculature has appropriated the ischium if we may rely on innervation for its identification).

Now there are indications that the characteristic mammalian mode of linkage is still in a state of flux, at any rate in Marsupialia, Rodentia and perhaps Carnivora. In certain members of these orders M. flexor cruris caput dorsale

[1] And *Elephantulus* (cf. footnote 3, p. 384).

is inserted laterally near biceps, whereas usually in mammals it is inserted near semitendinosus, or is implanted on that muscle by a tendinous intersection. In *Phalangista* and *Thylacinus* Cunningham has described complicated interconnections between the heads of origin and insertion; while I have found a condition approaching the more usual mammalian arrangement with a

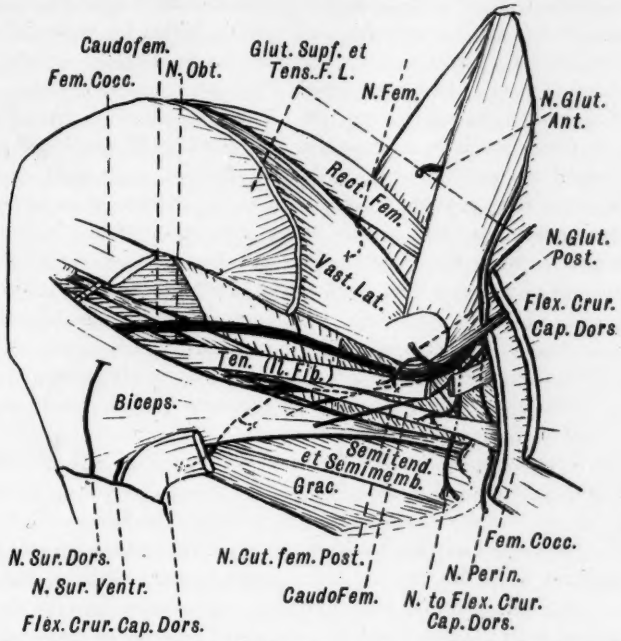


Fig. 15. *Erethizon dors.* × ¾. Left thigh. Position and dissection similar to that of *Tupaia* in fig. 4. A primitive eutherian muscular pattern is presented. Mm. caudofemoralis, iliofibularis (tenuissimus) and flexor cruris caput dorsale are all present with caudal origins. A M. femorococcygeus has, however, been differentiated from the superficial glutaeal musculature. This musculature is innervated from both Nn. glutaeus superior and glutaeus inferior as in therian mammals generally (cf. p. 424). M. flexor cruris caput dorsale is inserted laterally in the leg, a condition which parallels that found in various Marsupialia and all reptiles (figs. 3, 13 and 14) (*vide* p. 424). The relations of Nn. ischiadicus dorsalis, peronaeus, tibialis, cut. femoris posterior, ischiadicus ventralis, and pudendus to Mm. iliofibularis and caudofemoralis are like those of Tetrapoda generally (figs. 1 and 9). N. cut. surae lateralis is represented by Nn. surae dorsalis and surae ventralis as in many Insectivora and Primates (figs. 4, 5, 6, 8 and 10). The nerve to M. flexor cruris cap. dors. first passes ventrally to M. caudofemoralis as in all Amniota (figs. 9 and 13) before turning dorsally to its destination. The medially inserted portion of M. flexor cruris cap. ventr. is represented by a combined semitendino-semimembranosus (p. 422).

medial shank insertion in *Dasyurus* and *Perameles* (fig. 11). The rearrangement of muscle bellies in M. flexor cruris may have begun with the change of thigh movements which took place in Therapsid evolution; and the ambiguous connections between the hamstrings of some Marsupialia perhaps illustrate

the process of change. The condition in *Erethizon* cannot be claimed as a necessarily primitive feature.

Crocodilia differ from other reptiles in showing additional muscle bellies suggestive of a transitional step towards the mammalian scheme of cleavage. The medially-inserted part has an additional dorsal head (Gadow's flexor tibialis internus I, 3, Taf. XIX) like the mammalian "caudal head of semitendinosus," while the laterally-inserted part is joined by musculature from the ventral head (Gadow's flexor tibialis internus III), simulating the mammalian biceps (apart from its relation to gastrocnemius).

The differences between the respective insertions of the dorsal and ventral heads of M. flexor cruris in mammals and reptiles are thus bridged by intermediate conditions and are explained as a changed manner of cleavage in the flexor mass; they provide no objection to the identification of the dorsal and ventral heads on the basis of their innervation from N. ischiadicus ventralis, and support the view that its distribution to superficially-placed musculature at any rate has changed solely in reference to varied extensions and cleavages of M. flexor cruris. The transference of the lateral site of insertion across the lateral head of gastrocnemius, which is thus claimed as a mammalian characteristic, may be paralleled by many instances, such as the lateral shifting of sartorius across the iliopsoas in mammalian evolution; it is thus that M. biceps femoris was formed.

Various errors appear in the literature in regard to the homologies of reptilian and mammalian hamstrings, apart from those already noted in reference to the caput dorsale of M. flexor cruris in Monotremata and in Theria. Leche singled out the two-headed flexor tibialis internus of Chelonia for comparison with the two-headed semitendinosus of many Insectivora, while Gregory and Camp have compared the similar semitendinosus of Perissodactyla with the flexor tibialis externus of *Sphenodon* (supposing flexor tibialis internus to be the semimembranosus). The above comparisons involve our overlooking the various forms taken by M. flexor cruris cap. dors. in mammals as well as the varied patterns of M. flexor cruris in reptiles. Further, in respect of Chelonia and Insectivora an alteration in the nerve supply of the ventral head would have to be assumed. As Gadow has pointed out, comparisons of individual hamstrings in modern reptiles and mammals have little value (1882, p. 402); there has been considerable alteration of cleavage planes in the M. flexor cruris of mammals.

M. biceps has been invariably regarded as belonging to the dorsal thigh musculature (p. 404) and as an approximate equivalent of the tetrapod M. iliofibularis. This view was taken by Humphry and Leche, and by Gadow also, despite his recognition of M. tenuissimus as the representative of iliofibularis (1882, pp. 381, 385). Humphry, like various recent writers, overlooked the existence of the mammalian tenuissimus. He was misled into homologising the urodele iliofibularis with the mammalian biceps by the similarity of their insertions, and by his belief that the biceps of mammals

is commonly provided with a caudal head of origin (due, 1872, p. 167, to his mistaking the femorococcygeus of Leche for a part of biceps). Leche, on the other hand, appears to have been misled mainly by his observations on the innervation of biceps in Insectivora; these have been shown to require amendment (p. 391). He was further influenced by the frequent synergic association of biceps with femorococcygeus, e.g. among Insectivora. There is, however, reason to believe that the latter muscle has in these instances acquired an attachment near the knee-joint by distal migration from an insertion near the third trochanter (p. 405).

Romer (1922, p. 564) concluded by elimination that biceps femoris must represent the iliofibularis of other Tetrapoda; but he (like Pearson, 1926) omitted all consideration of tenuissimus as a representative of iliofibularis.

Objections to the derivation of biceps from iliofibularis may be summarised as follows: (1) innervation of biceps from N. ischiadicus ventralis, while that of iliofibularis is from N. ischiadicus dorsalis; (2) origin of biceps solely from ischium (rarely connected to vertebral column by M. flexor cruris cap. dors.); (3) biceps is ventral to M. caudofemoralis, iliofibularis is dorsal to it; (4) relations to N. cut. surae lateralis differ; (5) tenuissimus agrees in essential features with iliofibularis (p. 396). The only resemblance, indeed, between biceps and iliofibularis consists in the site of insertion, and even this differs in relations to cutaneous nerves.

The M. biceps femoris, thus found to present relations to nerves and muscles, showing it to be a part of M. flexor cruris caput ventrale, does not include the so-called "short head of biceps" of Edentata and Primates (shown by Parsons and Klaatsch to be a derivative of tenuissimus) (cf. p. 402); nor does it include the so-called "caudal head of biceps," more suitably described as M. flexor cruris cap. dors., for it is very commonly in mammals unconnected in any way with M. biceps femoris. The widespread belief in a former caudal origin for the mammalian biceps appears attributable less to the occasional connection with it of M. flexor cruris cap. dors. than to the description by Humphry, and subsequently by Parsons, of M. femorococcygeus in many mammals as a "part of biceps" (p. 408). The distinguishing features have been already pointed out.

The difference in the nerve supply of the "ischiofemoralis" of the orang-utan and the chimpanzee (and gorilla), pointed out by Fick (1895), and quoted by Kohlbrügge, suggests enquiry into the distinction between the nerves, viz. N. glutaeus posterior (*seu* inferior) and the "nerve to the hamstrings." Now Mm. caudofemoralis and tenuissimus, when present, pass between these nerves; but these muscles are absent in the large apes. In various Primates (figs. 8 and 10), however, one or other of these muscles is present and establishes the distinction between these nerves (e.g. in *Lemur*, *Tarsius*, *Hapale* and *Cebus*); and the nerve trunks of the apes bear an obvious topographical resemblance to them. It is concluded that in the orang-utan (fig. 10 B) the insertion of biceps has extended proximally on to the femur,

with the formation of a cleft between this and the more distally-attached part; but that in the chimpanzee and gorilla the "ischiofemoral" musculature is a partially differentiated femorococcygeus (as Leche surmised). The distribution of Nn. cut. femoris posterior and perinaealis confirm this conclusion (fig. 10); both are dorsal to the "ischiofemoral" of *Simia* but ventral to that of the chimpanzee, gorilla and gibbon. The union of these two cutaneous nerves in Man and certain apes has been already noted (p. 395).

*Distribution of N. ischiadicus ventralis to deep muscles.* Monotremata have a short muscle presenting a close resemblance to the ischiotrochantericus (Osawa) of reptiles, and the ischiofemoralis of urodeles (de Man) and of birds (Gadow). A comparison with other mammals points to the derivation of the gemelli, obturator internus and quadratus femoris from this musculature within the class of mammals, various marsupials, for example, having no obturator internus. In many Marsupialia the "nerve to quadratus femoris" is continued to supply a more distally-attached muscle, described by Cunningham as "adductor magnus." The distal extension of musculature thus indicated by a consideration of the distribution of N. ischiadicus ventralis is present also in specimens of *Putorius put.*[1] (*var. dom.*), *Meles tax.* and *Cebus* (fig. 10 D), and has been described as an anomalous condition in Man (Wilson, 1889), and may be appropriately termed "quadratus longus" in reference to its probable phylogenetic origin. It offers an analogy to the more distally-attached deep musculature (M. obturator posterior, p. 414) of urodeles and lizards (fig. 12 A), which receives its nerve supply through N. ischiadicus ventralis. Cunningham assumed the marsupial musculature so innervated to be "a part of adductor magnus," and entertained a doubt as to the value of nerve-supply for muscle homologies (1881, p. 270). But the hypothesis that the "quadratus longus" has been differentiated from M. quadratus femoris by distal extension of the insertion meets the facts of nerve-distribution as well as of topographical relations, and permits our regarding the difference of nerve-distribution as the outcome of adaptive changes in musculature paralleling those seen in the formation of the Lacertilian ischio-femoralis of Gadow (cf. p. 414).

(ii) *Aves.* The birds present a simple arrangement of muscle innervated from N. ischiadicus ventralis. Apart from the single deep muscle (Gadow's "ischiofemoralis") comparable with the M. ischiotrochantericus (Osawa) of reptiles and monotremes, there are two which pass to the shank, Mm. caud-ilio-flexorius and ischioflexorius Gadow, situated respectively dorsal and ventral to the caud-ilio-femoralis (the avian M. caudofemoralis *mihi*). The "accessorius" of the caud-ilio-flexorius (Gadow, 1891, p. 163) was regarded by Gadow as a remnant of a former extensive femoral insertion; but, as Romer has pointed out (1923, p. 549), there is no direct evidence that such has existed in reptiles, and a survey of Tetrapoda as a whole supports this criticism. It appears rather to be a caenotelic femoral insertion comparable with the

[1] Observation communicated by Mr W. A. Fell of the Cambridge University Anatomy School.

proximal extension of the insertion of semimembranosus (with differentiation of a praesemimembranosus) in many mammals; the similarity of its innervation with that which supplies a distal part of M. flexor cruris in Urodela, Crocodilia and Marsupialia (p. 374) is consistent with this interpretation. While this innervation does not exclude Romer's account of this accessorius muscle as a separated slip of gastrocnemius, this interpretation is less probable than that here adopted, viz. its being a part of M. flexor cruris, because (1) M. flexor cruris is sometimes partly innervated by nerve bundles passing dorsally to M. caudofemoralis *mihi*; (2) flexor cruris has acquired a similar attachment in other groups; and (3) the nerve to accessorius is not closely associated, in *Rhea amer.* (Gadow) at any rate, with the nerves to gastrocnemius.

(iii) *Salientia.* Noble has given an account of the derivation of the numerous muscles of Salientia from the less numerous muscles of Urodela. Though no satisfactory criterion was advanced for the distinction between superficial and deep flexor muscles, yet the muscles supplied in urodeles from N. ischiadicus ventralis are found to be represented in the frogs by long and short muscles supplied from the nerve which has been identified as their N. ischiadicus ventralis (p. 377).

### C. SOME PHYLOGENETIC MUSCULAR CHANGES AMONG TETRAPODA

(*a*) *Urodele specialisation.* There is reason to believe that the thigh structure in modern Urodela differs in some respects from that in the early Amphibia from which Amniota seem to have been derived. The femur has become more slender, but it is not clear that this can in all instances be regarded as a means of providing a relative lengthening of the stride. The large ventral "adductor" crest, as well as certain other prominences, are inconspicuous in modern Urodela; this is possibly related to their small absolute size.

The length of stride exhibited by terrestrial Urodela such as Salamanders is observed to be far greater in proportion to their size than the estimated stride of the earlier Tetrapoda. It approximates to the width of the track (as it probably did in the later Therapsida, e.g. Dicynodontia—Watson, 1917, p. 36). Even in Pelycosauria the stride was still so short as to be less, probably than half the width of the track (Watson, 1917, p. 14). The range of movement at the knee-joint of the Salamander has become greatly increased, and the knee can be straightened out, whereas in early Tetrapoda it was permanently crooked with a small range of movement.

It is concluded that some modification has occurred in superficial ventral thigh muscles of Urodela to which the extensive distribution of N. ischiadicus ventralis may be attributed (p. 416). In them again, there is a rectus internus (Humphry). There is no reason to believe that either this or the pubotibialis (with metazonal innervation) were ever present in the pro-Reptilia. A study

of modern Urodela moreover points to a progressive differentiation of M. pubotibialis, with the formation of an "adducteur du femur" (Perrin), perhaps better distinguished as a distinctive urodele formation by the term *M. pubifemoralis* (fig. 12). The femoro-fibular muscle (Humphry) of urodeles appears to be a caenotelic structure, being apparently unrepresented in Salientia and Amniota. There is, again, no definite evidence that the forerunners of Amniota ever possessed the caudocrural muscle (of Humphry), which has probably been derived in Urodela from a common caudofemoral mass along with the caudalifemoralis (of de Man) (pp. 409, 421)[1].

(*b*) *Amniota.* The principal features of the post-axial region of Amniota consist in the great extension of distribution of N. cutaneus femoris posterior, and in the acquisition by the hamstring musculature (M. flexor cruris) of a dorsal head of origin in addition to the ventral head possessed by Urodela (figs. 13 A and B). It is recognised in both birds and mammals, and though direct confirmatory evidence from fossil remains is difficult to obtain, it may have been present in the Cotylosauria. The site of attachment of this dorsal head varies, being caudal in *Sphenodon* and Lacertilia (fig. 14), iliac in Chelonia and Crocodilia, variable in birds, and caudal in mammals (possibly secondary to an earlier iliac attachment).

Lacertilia and Crocodilia are characterised by the more extensive origin and large size of M. caudofemoralis, and by the formation of a plane of cleavage in the muscle, separating parts named "caudifemoralis" and "caudi-ilio-femoralis" by Gadow. This muscle has an additional insertion by a long tendon to the knee-joint region, a feature shared with *Sphenodon*. Features which distinguish the evolutionary trend in mammalian thigh structure from that of modern reptilian groups may be summarised as follows:

(1) The small size in mammals of M. caudofemoralis, and its complete loss in some of them, and its variability in site of distal attachment and in function (figs. 4, 5, 11, 12 and 14).

(2) Absence of a plane of cleavage in M. caudofemoralis, or of a long knee-tendon like that of the M. caudofemoralis of most reptiles (fig. 3).

(3) Shifting of the origin of M. caudofemoralis in some mammals (fig. 5) from the caudal vertebrae to the ischium (it occurs in a limited fashion in Crocodilia).

(4) The small size of the dorsal head of M. flexor cruris in most mammals, and its medial attachment in the leg; the large size and characteristic mode of cleavage of the ventral head of M. flexor cruris into Mm. biceps, semitendinosus and semimembranosus, and the attachment of this ventral head on both medial and lateral sides in the leg. The characteristic mammalian conditions of M. flexor cruris are only partially illustrated in *Erethizon*, Monotremata and various Marsupialia (cf. figs. 6 and 15).

(5) The large size of M. iliofemoralis and an associated change in the form

[1] The attachments of the caudocrural and the course of N. perinaealis (p. 374) favour this interpretation rather than a derivation of the caudocrural from the ischio-caudal.

of the os coxae (the ilium being "pre-acetabular"), and the differentiation of this muscle into Mm. glutaeus superficialis and profundus (fig. 12) with associated differentiation of the third and great trochanters.

Of these M. glutaeus superficialis has in the more specialised Theria undergone great expansion of the insertion, with differentiation in many instances of distinct Mm. tensor fasciae latae and femorococcygeus. M. glutaeus profundus undergoes delamination in Theria into a superficial M. glutaeus medius and a deep M. glutaeus minimus, and often also accessory muscles such as pyriformis. In various mammals a sacro-tuberous ligament makes its appearance as a fibrous arcade providing origin for the more caudal part of M. femorococcygeus.

(6) The small size of M. iliofibularis (i.e. "tenuissimus"), and its loss in some mammals including most of those with the more specialised limbs. It is wanting in Monotremata.

(7) Probable absence of any N. cutaneus femoris ventralis, and the frequent representation of N. cutaneus surae lateralis in Insectivora, Rodentia and Primates by two nerves, Nn. surae dorsalis and surae ventralis. This arrangement, however, has become modified in certain apes and in Man.

## D. RÉSUMÉ AND CONCLUSIONS

Re-examination of the post-axial region of the tetrapod thigh has shown that extensive confusion in the nomenclature employed in published accounts renders its revision imperative for phylogenetic studies. Among mammals at least four names have been given to M. caudofemoralis (Leche), others being "praesemimembranosus" (or "condylar slip of semimembranosus"), "pyriformis" and "ischiofemoralis" (Murie). On the other hand, the name "caudofemoralis" has been applied to three different muscles in mammalian literature, viz. (1) in Leche's sense, (2) to M. femorococcygeus—Leche, and (3) to M. flexor cruris caput dorsale (by Forster). The name "ischiofemoralis" has been applied to one muscle in Urodela, to two others in reptiles[1] and to yet four other muscles among mammals. The so-called "short" and "caudal" heads of biceps require distinction from "biceps femoris" *sensu stricto*. Much confusion also attends the use of the term "adductor magnus," owing to its frequent application to semimembranosus derivatives.

Amendment of observations has been found necessary in regard to (1) Leche's account of the innervation of biceps femoris in Insectivora (p. 391), (2) Parsons' account of the innervation of glutaeus maximus in Rodentia (p. 406), (3) Gadow's account of the innervation of his "pubi-ischio-femoralis" posterior (Hauptheil) in Crocodilia (p. 414), (4) Gadow's account of his "flexor tibialis externus" in Lacertilia (p. 416).

[1] If the distinctive character of the innervation is relied upon, the muscle so named is in part (p. 414) a derivative of M. obturator posterior in Lacertilia, but belongs to the diazonal sphere (M. adductor) in Crocodilia and Chelonia.

The following homologisations have been rejected for reasons stated above, but which cannot be here considered individually, from considerations of space:

(1) Humphry's comparison of the urodele caudocrural intersection with the ilio-ischiadic ligament of reptiles and the semitendinosus intersection of mammals (p. 421).

(2) Bland Sutton's derivation of the reptilian caudi-femoralis from the caudo-crural (Humphry) and of the long tendon from flexor musculature (p. 418).

(3) Gadow's comparison of the urodele caudocrural with the reptilian flexor tibialis externus (1882, p. 402) (p. 419).

(4) Gadow's comparison of the reptilian caudi-ilio-femoralis with the human pyriformis (p. 408).

(5) Comparison by Meckel, Macalister and others, of the eutherian pyriformis with M. caudofemoralis (Leche) of other mammals (p. 408).

(6) Description of the large buttock muscle of Monotremata (M. flexor cruris caput dorsale, p. 416) as a "glutaeus maximus" by most writers (p. 420).

(7) Comparison of the urodele iliofibularis with the mammalian biceps femoris by Humphry, and of the latter muscle with the sauropsid iliofibularis by Gadow (1882, pp. 381, 385) (*vide* p. 424).

(8) Leche's derivation of biceps femoris from dorsal thigh musculature (p. 424).

(9) Confusion of M. caudofemoralis (Leche) with femorococcygeus, and the application of the term "agitator caudae" to each of them (by Humphry and Macalister respectively).

(10) The claims of Perrin and Osawa that the dorsal head of M. flexor cruris in *Sphenodon* is comparable with the caudi-ilio-femoralis of other reptiles (p. 418).

Following on these rejections, various inferences of recent writers are also rejected, viz.:

(1) Forster's derivation of M. flexor cruris caput dorsale from glutaeal musculature (p. 420).

(2) Comparison by Gregory and Camp of the cat's femorococcygeus with M. caudofemoralis (Leche) of *Echidna*; and of the cat's pyriformis with M. caudofemoralis of *Ornithorhynchus*, with M. caudi-ilio-femoralis of reptiles and with M. flexor cruris caput dorsale (*mihi*) of *Sphenodon* (pp. 407, 408, 424).

(3) Romer's adoption of the terms "coccygeo-femoralis brevis," "caudi-ilio-femoralis" and "pyriformis" as synonymous, and his comparison of the urodele caudo-crural and the reptilian caudifemoralis with mammalian "caudal slips of hamstrings" (p. 418).

(4) Pearson's derivation of the monotreme M. flexor cruris caput dorsale (her "crurococcygeus") from M. caudifemoralis (p. 420).

(5) The inference of Humphry (1872, p. 167) and Bland Sutton that biceps femoris of mammals had formerly a caudal origin[1], and their account of the origin of the lig. sacro-tuberosum (pp. 408, 425).

Re-examination of the animals in question has shown that the study of tetrapod myology simply by perusal of published descriptions must lead to many erroneous inferences; the following merit immediate correction:

(1) Apparent variation in nerve supply of sartorius in Rodentia (Parsons, 1894, p. 282), through confusion with M. tensor fasciae latae. Sartorius is found absent in *Erethizon dors.*

(2) Apparent caudal origin of semimembranosus in many Rodentia (Parsons, 1894, p. 285), owing to confusion with M. caudofemoralis; and apparent lack of an ischial head to semitendinosus, owing to confusion with M. flexor cruris caput dorsale (*mihi*).

(3) Apparent difference of innervation of "adductor magnus" in Insectivora and Rodentia, owing to its confusion in the latter order with semimembranosus musculature.

(4) Apparent innervation of "biceps" in Rodentia (Parsons, 1894, pp. 282, 284) through N. glutaeus inferior, as well as through the nerve to the hamstrings, owing to confusion with M. femorococcygeus; and Parsons' error regarding the nerve supply of M. glutaeus maximus (p. 406).

(5) Apparent differences between muscles and nerve supplies of Menotyphla and other Insectivora (p. 391).

(6) Apparent differences between *Echidna* and *Ornithorhynchus* in respect of Mm. "pyriformis" and caudofemoralis, as set out by Gregory and Camp (1918, pp. 497, 499), owing to terminological confusion (p. 414).

(7) Apparent difference in attachments of M. glutaeus maximus of Monotremata and other mammals (Leche, 1883, p. 72, and Frets, 1909, pp. 74, 90), due to erroneous identification (p. 420); and the innervation in Monotremata of supposed "M. glutaeus maximus" through N. tibialis (recorded by Westling, 1890, p. 55, but questioned by Frets, 1909, p. 94, Westling's account incorrectly making it appear that a N. glutaeus inferior passes deep to M. caudofemoralis—Leche).

(8) Passage of N. ischiadicus ventral to a supposed "pyriformis" of Monotremata (Frets, 1909, p. 93), unlike the relation in Eutheria (p. 394); apparent absence of a M. caudofemoralis (Leche) in Monotremata and Marsupialia; an apparently long phylogenetic history for M. pyriformis and its more distal attachment in Monotremata than in Eutheria. These errors follow from mistaken description of M. caudofemoralis as "pyriformis" in non-eutherian mammals (p. 413).

[1] Humphry attributed to M. biceps femoris an iliac attachment (in mammals through the sacro-tuberous ligament), an error due partly to his confusion of this muscle with M. iliofibularis (p. 424 *supra*). The "caudal head of biceps," described by Parsons and other writers in Rodentia and various other mammals, is not M. biceps in the usual sense of the term (as employed in Man); it is a M. femorococcygeus (*vide* p. 408 *supra*).

(9) Apparent difference between Lacertilia and *Sphenodon* in the proximal attachment of Gadow's flexor tibialis externus, due to error in description of Lacertilia (p. 416).

(10) Absence in Chelonia alone among modern reptiles of a M. caudi-femoralis (cf. p. 419); absence in Crocodilia of any M. pubi-ischio-tibialis (as Gadow suggested—1882, p. 404, footnote, it is perhaps included in his "flexor tibialis internus"); variable innervation of M. ischiofemoralis (p. 429) and variable insertion of Mm. iliofibularis (p. 403) and pubi-ischio-femoralis posterior (p. 414) in reptiles, according to Gadow's account.

(11) Apparent resemblance of urodeles and certain mammals in possession of a "short head of biceps"; the muscle so named is clearly a caenotelic structure in each group (pp. 403, 428).

(12) M. tenuissimus apparently confined to mammals (but now shown to be the iliofibularis of other tetrapods (pp. 403, 425).

(13) Apparent derivation of the mammalian glutaeus medius from the reptilian iliofibularis (Frets, 1909, p. 94), due to his mistaking the monotreme M. glutaeus superficialis for a glutaeus medius and to an unwarranted reliance on the site of separation of nerve bundles for their identification (p. 420).

## E. GENERAL CONCLUSIONS

1. All classes of Tetrapoda present a similar topographical arrangement of structures in the post-axial region of the thigh; the similarity is largely obscured in the literature by diverse systems of nomenclature (*vide* Résumé, p. 429 *supra*).

2. The main nerve trunks have retained similar courses relative to muscles despite great differences in the size of these muscles; this is true of cutaneous as well as of muscular nerves. Variations are greatest among Urodeles.

3. Considerable variation occurs in the sites of separation of nerve bundles; thus we find a N. fibularis in Urodela, formed by the delayed separation of N. ischiadicus dorsalis (*mihi*) from N. peronaeus.

4. The distribution of nerves, defined by their course in the thigh, remains approximately constant; muscle migration or extension appears adequate to account for modifications of nerve distribution, e.g. the innervation of M. flexor cruris caput dorsale (*mihi*) in Amniota from N. ischiadicus ventralis (*mihi*), as a result of dorsal extension of musculature and of its nerve supply.

5. Despite the vestigial character of Mm. caudofemoralis and iliofibularis in mammals, the relations of adjacent nerves remain essentially the same as in other Tetrapoda; this is true also of the vestigial M. caudofemoralis of Salientia and Aves.

6. Some instances are found in which there have been phylogenetic alterations of the courses of nerve bundles (pp. 397, 403, 409); in some instances, though not in all, the changes are the outcome of adaptive modification of

the musculature, while the loss in Salientia of a diazonal pelvic nerve may be attributable to adaptive modification of the skeleton.

7. The reptilian iliofibularis muscle has been handed on to the mammals as the "tenuissimus." Further evidence is found in support of the view deriving the "short head of biceps" of certain mammals from the tenuissimus (fig. 10).

8. The mammalian biceps femoris is a derivative of ventral thigh musculature (M. flexor cruris, *mihi*) and has not been derived from the reptilian or urodele iliofibularis. The widespread belief that its origin was primitively caudal in mammals is partly traceable to the frequent erroneous description of the femorococcygeus as a part of biceps. The sacro-tuberous ligament is not derived from the biceps muscle.

9. The possession not only of a ventral head but also of a dorsal head by M. flexor cruris distinguishes the Amniota from the Amphibia, but this head is usually vestigial and sometimes absent in mammals (figs. 8, 11 and 13).

10. The so-called "glutaeus maximus" (Westling and others) of Monotremata is a part of the hamstring musculature, viz. M. flexor cruris caput dorsale; it is the homologue of the "caudal head of semitendinosus" in Theria. The very similar musculature of reptiles is approximately that described by Gadow as "flexor tibialis externus," by Humphry as "biceps."

11. The pyriformis is a neomorph in certain eutherian orders, and no muscle homologous with it is found in Monotremata or Marsupialia.

12. The caudofemoral retractor musculature of Urodela, Reptilia and early Tetrapoda is still represented by vestigial muscle slips in frogs, birds and mammals.

13. Much confusion exists in myological literature through the use of names in different ways, viz. Mm. caudo- and caudi-femoralis, pyriformis, biceps, (prae-) semimembranosus, adductor magnus, glutaeus maximus, coccygeo-femoralis brevis, and N. cutaneus femoris posterior, N. glutaeus inferior, etc.

14. The omission from consideration of the existence in mammals of a tenuissimus, a femorococcygeus and a caudofemoralis, has been largely responsible for various erroneous conclusions reached by recent writers.

15. Monotremata resemble other mammals and differ from reptiles in (1) the functional replacement of M. caudofemoralis by derivatives of M. iliofemoralis and by the ventral head of M. flexor cruris in the action of thigh retraction: related therewith are characteristic changes in the form of the ilium, ischium and femur; (2) the reduction of M. iliofibularis; (3) the mode of cleavage of M. flexor cruris. They fail to show various features found in many Theria: (1) lack of extension of M. ischiotrochantericus and of its differentiation into obturator internus, gemelli and quadrate muscles, (2) lack of extension of M. glutaeus superficialis with differentiation of Mm. tensor fasciae latae and femorococcygeus, (3) lack of reduction in size of M. flexor cruris caput dorsale (fig. 14).

## TABLE OF SYNONYMS[1] AND HOMOLOGIES

| | *M. flexor cruris* (*N. ischiadicus ventralis*) | | *M. caudofemoralis* (*N. pudendus*) | |
|---|---|---|---|---|
| TETRAPODA | CAPUT VENTRALE | CAPUT DORSALE | | |
| Urodela | Pubotibialis, puboischiotibialis, ischioflexorius | Wanting | Caudalifemoralis et caudalipubo-ischiotibialis (p. 428) | de Man |
| | Semitendinosus and semimembranosus | Wanting | Caudofemoralis | Humphry |
| Salientia | Graciles major et minor, sartorio-semitendinosus, adductor magnus cap. ventr. | Wanting | Pyriformis et caudalipuboischio-tibialis (p. 409) | Noble |
| Rhynchocephalia | Adductor superficialis (*partim*), flexor cruris superficialis et flexor cruris profundus | Flexor cruris profundus (caud. Teil) | Femorocaudalis | Frets |
| Lacertilia | Flexor tibialis internus et pubi-ischio-tibialis (*partim*) | Flexor tibialis externus (caudal part not recognised) | Caudi-femoralis et caudi-ilio-femoralis | Gadow |
| Crocodilia | Flexor tibialis internus II and III | Flexor tibialis internus I, 3 et flexor tibialis externus | Caudi-femoralis et caudi-ilio-femoralis | Gadow |
| Aves | Ischio-flexorius<br>Semimembranosus | Caud-ilio-flexorius<br>Semitendinosus | Caudi-ilio-femoralis<br>Adductor longus | Gadow<br>de Man |
| Monotremata | Semimembranosus, semitendinosus et biceps | Glutaeus maximus | Pyriformis | Meckel, Frets |
| | — | "Crurococcygeus" | Pyriformis<br>Quadratus femoris<br>Caudofemoralis | Pearson<br>Coues<br>Westling |
| Marsupialia | Semimembranosus, semitendinosus et biceps (cap. isch.) | Caudal head of biceps | Pyriformis | Parsons, Macalister, Romer |
| | — | — | Pyriformis et ischiofemoralis | Cunningham |
| Eutheria | Semimembranosus<br>Semitendinosus I et biceps | Semitendinosus 2 | Caudofemoralis | Leche |
| | — | — | Ischiofemoralis | Murie, 1865 |
| | — | — | Crurococcygien | Cuvier (genet and mole) |
| | — | — | Pyriformis | Woollard |
| | — | — | Caudofemoral | Humphry and Macalister |

| TETRAPODA | *M. iliofemoralis* (*Nn. femoralis et ischiadicus dorsalis*) | *M. flexor profundus* (*N. ischiadicus ventralis*) | |
|---|---|---|---|
| Urodela | Ileofemoralis | Ischiofemoralis et pubi-ischio-femoralis externus (*partim*) | de Man |
| Rhynchocephalia | Iliofemoralis | Ischiotrochantericus et pubi-ischio-troch. externus (*partim*) | Osawa |
| Crocodilia | Iliofemoralis | Pubi-ischio-femoralis posterior (*partim*) | Gadow |
| Aves | Iliofemorales | Ischio-femoralis | Gadow |
| Monotremata | Glutaeus medius et glutaeus minimus; iliacus (?) | Obturator internus | Coues |
| | — | Obturator B | Pearson |
| | — | Quadratus femoris | Westling |
| Theria | Glutaeus superficialis, tensor fasciae latae et femorococcygeus glutaei medius et minimus, pyriformis; iliacus (?) | — | Leche |
| | — | Quadratus femoris, gemelli et obturator internus and occasionally another muscle ("adductor magnus"—Cunningham in certain Marsupialia) | Kohlbrügge |

[1] The more important synonyms, only, can be tabled here. Certain others are mentioned in the text.

## TABLE OF SYNONYMS AND HOMOLOGIES (*continued*)

| TETRAPODA | *M. extensor iliotibialis* (*Pars anterior*) (*N. femoralis*) | *M. extensor iliotibialis* (*Pars posterior*) (*N. ischiadicus dorsalis*) | *M. iliofibularis* (*N. ischiadicus dorsalis*) | |
|---|---|---|---|---|
| Urodela | Ileotibialis | | Ileofibularis | de Man |
| | Iliotibialis | Ilioextensorius | Iliofibularis | Noble |
| Salientia | Iliacus internus, iliacus externus et tensor fasciae latae | Cruralis et glutaeus | Iliofibularis | Noble |
| | — | — | Biceps (lang. Kopf) | Nussbaum |
| Rhynchocephalia | Extensor triceps | | Ileo-fibularis | Osawa |
| Lacertilia | Extensor ilio-tibialis | | Iliofibularis | Gadow |
| Crocodilia | Extensor ilio-tibialis et iliofibularis II | | Iliofibularis I | Gadow |
| Chelonia | Vastus femoris (cap. long.) | Glutaeus maximus | Glutaeus minimus | Ogushi |
| Aves | Ilio-tibialis | | Ilio-fibularis | Gadow |
| Mammalia | Rectus femoris | Probably wanting (p. 407) | Tenuissimus (often wanting) | Leche |

## LIST OF ABBREVIATIONS IN FIGURES

| | |
|---|---|
| *A. Isch.* | Arteria ischiadica |
| *Caudocrur.* | Caudocrural |
| *Caudofem.* | Caudofemoralis |
| *Cocc.* | Coccygeus |
| *Extens. Il. Tib.* | Extensor iliotibialis |
| *Fem. Cocc.* | Femorococcygeus |
| *Fem. Fib.* | Femorofibularis |
| *Fem. Tib.* | Femorotibialis |
| *Flex. Crur. Cap. Dors.* | Flexor cruris caput dorsale |
| *Flex.Crur.Cap.Ventr.* | Flexor cruris caput ventrale |
| *Glut. Med.* | Glutaeus medius |
| *Glut. Prof.* | Glutaeus profundus |
| *Glut. Supf.* | Glutaeus superficialis |
| *Grac.* | Gracilis |
| *Il. Extens.* | Ilioextensorius |
| *Il. Fem.* | Iliofemoralis |
| *Il. Fib.* | Iliofibularis |
| *Il. Tib.* | Iliotibialis |
| *Isch. Caud.* | Ischiocaudalis |
| *Isch. Flex.* | Ischioflexorius |
| *Isch. Troch.* | Ischiotrochantericus |
| *Lig. Sac.-Tub.* | Ligamentum sacro-tuberosum |
| *N. Cut. Fem. Post.* | Nervus cutaneus femoris posterior |
| *N. Cut. Sur. Lat.* | Nervus cutaneus surae lateralis |
| *N. Cut. Sur. Med.* | Nervus cutaneus surae medialis |
| *N. Fem.* | Nervus femoralis |
| *N. Fib.* | Nervus fibularis |
| *N. Glut. Ant.* | Nervus glutaeus anterior |
| *N. Glut. Post.* | Nervus glutaeus posterior |
| *N. Isch. Dors.* | Nervus ischiadicus dorsalis |
| *N. Isch. Ventr.* | Nervus ischiadicus ventralis |
| *N. Perin.* | Nervus perinaealis |
| *N. Peron.* | Nervus peronaeus |
| *N. Pud.* | Nervus pudendus |
| *N. Sur. Dors.* | Nervus surae dorsalis |
| *N. Sur. Ventr.* | Nervus surae ventralis |
| *N. Tib.* | Nervus tibialis |
| *Obt. Post.* | Obturator posterior |
| *Pect.* | Pectineus |
| *Praesemimemb.* | Praesemimembranosus |
| *Pub. Fem.* | Pubifemoralis |
| *Pub. Isch. Tib.* | Pubi-ischio-tibialis |
| *Rect. Fem.* | Rectus femoris |
| *Qu. Fem.* | Quadratus femoris |
| *Qu. Long.* | Quadratus longus |
| *Semimemb.* | Semimembranosus |
| *Semitend.* | Semitendinosus |
| *Tens. F. L.* | Tensor fasciae latae |
| *Tenuiss.* | Tenuissimus |
| *Tr. Tert.* | Trochanter tertius |

## LIST OF FIGURES

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2. *Salamandra mac.* Post-axial region of thigh. p. 378
3. *Alligator miss.* Post-axial region of thigh. p. 380
4. *Tupaia pict.* Post-axial region of thigh, and glutaeal region. p. 385
5. *Macroscelides* sp. Post-axial region of thigh, and glutaeal region. p. 386
6. *Talpa eur.* Post-axial region of thigh, and glutaeal region. p. 389
7. *Lutra vulg.* Post-axial region of thigh, and glutaeal region. p. 392
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# THE MUSCULATURE OF THE HEART, WITH ITS APPLICATION TO PHYSIOLOGY, AND A NOTE ON HEART RUPTURE

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## INTRODUCTION

From the anatomical point of view the muscle fibres of the heart have been investigated in two divisions, fibres of the ventricles, and fibres of the auricles. The arrangement of the former was extensively studied by earlier writers, and was finally placed on a definite basis by MacCallum (1900) and Mall (1911); the latter were observed at an earlier date by Henle (1876), and more recently by Papez (1920). These writers investigated the subject from a purely anatomical aspect, and so could divide it in this manner.

From the point of view of function, however, one has to consider them together, and in 1907 Keith wrote on the subject in this way but mainly from the physiological aspect. The observations of Lewis (1917) on the times of contraction of various parts of the heart are also included in the physiological side of the question.

The work upon which this paper is based has consisted in the dissection of muscle fibres of the auricles and ventricles in both adult and foetal human hearts. From the anatomical point of view my findings have been largely confirmatory of the articles of Mall and Papez, but in the following pages I have endeavoured to correlate the anatomical findings with the physiological observations put forward by Keith and Lewis. Also in this connection, some statements of Pettigrew's (1864) on the anatomy of the right ventricle of the bird have been applied to the action of the human right ventricle.

While investigating the left ventricle, I was so struck with the thinness of the apex, especially in dilated hearts, where there is even less protection, that I was led to consider the question of spontaneous rupture of the heart. Four

specimens were obtainable from the Pathological Museum through the kindness of Dr A. Murray Drennan, and these are described here, without, however, any clinical details.

In presenting the following observations and comments, I desire to take this opportunity of expressing my thanks to Professor W. P. Gowland for permission to use the material on which the main part of this paper is based.

## HISTORY OF THE LITERATURE

The literature of the musculature dates from the middle of the seventeenth century, when Nicolaus Stensen and Lower investigated the heart from this point of view. The former laid down four rules: (1) The muscle fibres are fleshy in the middle and tendinous at their extremities; (2) The superficial fibres descend to the apex, where they become deep and ascend; (3) The apex of the heart is not closed by muscle but by the serous membranes; (4) The apex is in the shape of a star. Lower recognised the formation of loops fixed at both ends to the fibrous rings. In 1681, Borelli studied the heart muscle, and gave an anatomical explanation for its contraction.

The next observer is Winslow, who, in 1711, stated the rule, which is quoted in almost every French textbook, "Le cœur est composé de deux sacs musculeux, renfermé dans un troisième également musculeux." He is followed by two other French anatomists, Lieutaud (1740) and Senac (1740), who both wrote works on the anatomy of the heart. Senac appears to have been the first to recognise the spiral arrangement, while Lieutaud considered it as being composed of two sacs, a small one, left ventricle, which occupies two-thirds of the cavity of the large one.

Haller, in his *Elementa Physiologiae* (1764), notes that the vortex is composed of two horns to correspond with the two main bands of muscle which there penetrate the heart. He traced them, one into the septum and the other to the base again by penetrating the left ventricle.

In 1780, Wolff made an addition by demonstrating some longitudinal fibres on the diaphragmatic surface. Mall (1911) has, however, shown that these are not always present, a fact confirmed by my own observations. No new investigations appear to have been made until 1823, when Gerdy, in his doctor's thesis, described the formation of figures of eight convex to the apex, noted the existence of interventricular bands, and studied the general arrangement of fibres. Since then, Gerdy's work has predominated in French textbooks.

For the next thirty years the literature increases rapidly, but, with the exception of Weber (1831), J. Reid, Searle (both in 1836), and Ludwig (1849), no new observations are made. Weber noted the circular fibres in the left ventricle; Reid gives a general account of the heart musculature derived from former observers, and especially from the manuscript of A. Duncan, Junr., on the hearts of the ox and sheep. Searle unrolled the muscle of the left ventricle, and Ludwig elaborated Gerdy's conception of the arrangement of the fibres in figures of eight. Bonamy and Beau of this period (1847) produced some

splendid plates, which are copied in French textbooks up to the present time (Poirier and Charpy, 1912).

About 1865, Pettigrew observed the gradational sequence in direction of the heart fibres, which Ludwig had previously mentioned; he also divided the heart wall into seven layers, separating the external fibres into anterior ones going to the anterior papillary muscle, and posterior ones going to the posterior papillary muscle. At this time Lindes (1865) points out in the embryo the separation of the aorta, from its origin, the right ventricle, by means of the membranous septum; also Winckler disputes Winslow's statement of two muscular sacs being contained in a third, and claims that there are no fibres proper to each ventricle.

Henle (1876) gave details of full investigation which he carried out himself on the muscle fibres in both auricles and ventricles. No better account of the musculature of the auricles appears until that of Papez in 1920.

The arrangement of the septum is made clear by the investigations of His, Senior (1886) and His, Junior (1891 and 1894), and in 1889 MacAlister notes: (1) the weakness of the apical region; (2) the degree of obliquity diminishing from the surface inwards; and (3) the presence of annular fibres. Krehl (1891) mentions the middle layer of the left ventricle, and describes it as a cylinder; he was the first to note the presence of the tendon of the conus.

Then, in 1900, appears MacCallum's paper on the unrolling of fibres in the heart of the foetal pig; Knower (1908) applied this to the human heart, and in 1911 Mall, in his comprehensive article, gives an account of the general anatomy and function of the muscle of the ventricles. Shaner (1924) follows this up with a paper on the musculature of the vertebrate ventricle.

These later articles lead to each other so naturally that, in recording them, the order has not been interrupted by referring to articles of a slightly different type. In 1891, Haycraft throws some light on the action of the ventricle, and Samways (1899) points out the muscular defence of the valvular orifices. Then Keith (1902 and 1907) studied the anatomy of the heart muscle from a functional point of view, and in the Harveian Lecture of March 1918, briefly summarises his results. Morison (1913) gives some general facts on the contraction of the auricles, and then Lewis (Croonian Lecture of 1917) details the results of his electrical experiments of the heart musculature.

## TECHNIQUE

The technique followed has been largely based on that of MacCallum (1900) and Mall (1911), and also of Shaner (1924) in his preparation of the heart of the fowl.

The specimens have been adult and foetal human hearts, some of which have been removed from cadavers embalmed for dissecting-room purposes, and have been in varying conditions between contraction and dilatation; others have been fresh hearts obtained at post-mortem.

The technique has been modified in different specimens.

1. Hearts from embalmed cadavers. These have been preserved in 3 per cent. carbolic acid for from four to seven years. Some of these have been dissected after soaking for 12 hours in water; other have been brought to the boil and then dissected. This softens the outer connective tissue and fat without making the heart assume a contracted condition.

2. Fresh hearts from post-mortems. These have been treated in one of three methods: (*a*) Some were boiled according to Mall's method for two hours, i.e. in water acidulated with acetic acid. This, however, puts them in the systolic state, and makes dissection difficult, although the superficial fat is much more easily removed; (*b*) Others have been preserved in 3 per cent. carbolic acid, and dissected after washing as above; (*c*) Another method has been boiling after filling out the cavities with cotton-wool. This is somewhat akin to Pettigrew's method (1864) of filling the ventricles with bran and then boiling the heart.

The best method for securing specimens I have found is to soak them in 3 per cent. carbolic acid for six months at least, as when properly permeated the muscle fibres are less brittle. The heart is then removed from carbolic acid, and the acid washed out in running water for 24 hours. Though the removal of pericardium and superficial fat is difficult, the fibre-bundles are much more easily reflected.

If sufficient hearts are available, however, it is instructive to prepare specimens by several methods, as then various conditions between contraction and dilatation are observed.

## INVESTIGATION

A heart is taken, prepared by any of the above-mentioned techniques, and the pericardium, epicardial fat and vessels are first cleaned off. This can be done in a superficial manner in the auriculo-ventricular grooves, and then the auricles can be separated from the ventricles. The two divisions of the heart can now be treated separately.

### *A.* VENTRICLES

The fat has now to be cleaned off right down to the muscular fibres of the heart wall; an easy matter if the heart has been boiled, less easy if soaked in carbolic acid for a long time, but difficult and tedious in a heart soaked in carbolic for only a few days. When this is done the aorta and pulmonary artery are cut off at the level of the semilunar valves; a view can now be obtained of the tendinous rings at the base of the heart, i.e. the rings surrounding the auriculo-ventricular orifices and giving attachment to the valves (fig. 1). The left auriculo-ventricular ring contains the aortic orifice as well as the auriculo-ventricular orifice, and so the elastic wall of this vessel can be removed without disturbing the continuity of the ring (MacCallum) (fig. 2). The two rings are joined together at the posterior aspect of the aorta, and from the septal wall of the aorta, the tendon of the conus (first described by Krehl, 1891) runs over the superior surface of the conus arteriosus. From these three tendinous masses

(fig. 2), the superficial fibres take origin. The muscle fibres of the ventricles may be described under three headings: (i) Superficial layer; (ii) Middle layer; and (iii) Deep layer. It may also be mentioned here that, in this description, the diaphragmatic surface of the ventricle will be spoken of as the posterior surface.

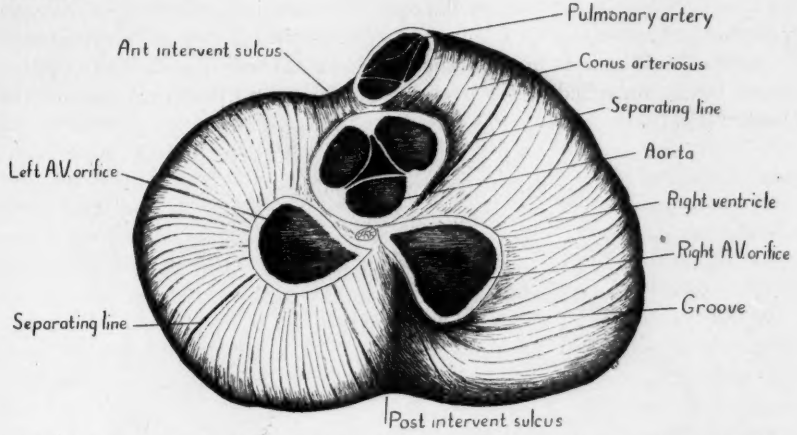



**Fig. 1.** Base of contracted heart showing orifices. Groove shown at the posterior margin of the right auriculo-ventricular orifice. Note the area of cross-section of the aorta (cf. fig. 2).

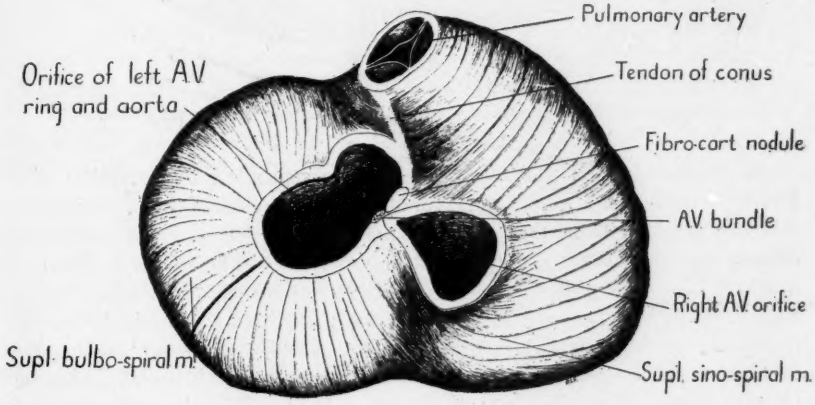



**Fig. 2.** Base of contracted heart, after removal of aorta, showing the three tendinous masses.

(i) ***Superficial Layer.*** These fibres run downwards, in general, from right to left across the anterior surface of the heart, and are divided into two groups.

(*a*) Those fibres taking origin from the anterior aspect of the tendons at the base of the heart are spoken of as the superficial bulbo-spiral band (Mall,

1911), and appear at the base of the heart on the anterior surface, and at the apex on the posterior surface.

(*b*) Those fibres taking origin from the posterior aspect of the tendons at the base, are spoken of as the sino-spiral band (Mall). They appear on the posterior surface, high up near the base; on the right margin, nearer the apex; and on the anterior surface, at the apex. From this it can be seen that the anterior surface at the apex is formed of sino-spiral fibres, and the posterior surface of bulbo-spiral fibres. As the apex has often been described as a vortex, these bands are called, respectively, the anterior and posterior horns of the vortex (fig. 3).

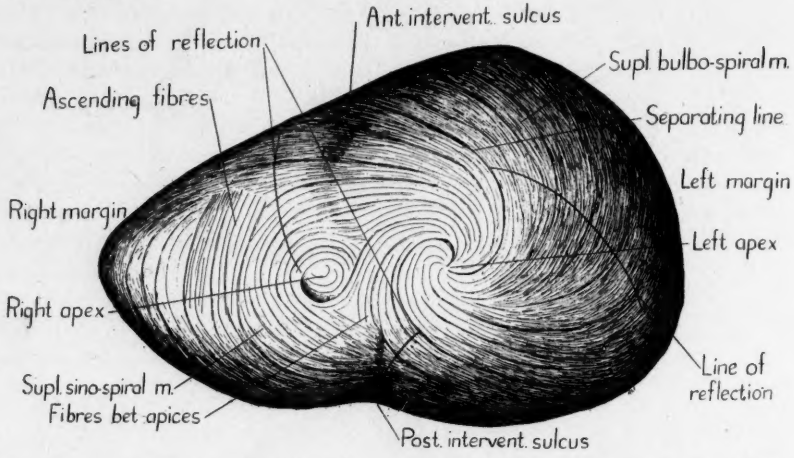



**Fig. 3.** Apex of dilated heart, showing the ascending fibres on the anterior surface of the right ventricle, and some superficial sino-spiral fibres passing between the apices.

For demonstration purposes these can be separated by removing with forceps in a "carbolic heart" one layer of fibres along each of the following two lines: (*a*) One line beginning at the left margin of the left auriculo-ventricular orifice, and then running very gradually downwards, almost horizontally at first and then more obliquely, across the posterior surface, forming the upper boundary of the superficial bulbo-spiral band; and then, at the right, turning round and downwards to the apex; (*b*) The other line beginning at the posterior end of the tendon of the conus at the angle between it and the aorta, running almost vertically down to the left margin a little distance above the apex, and then descending on the left margin to the apex. Fibres to the left of this are bulbo-spiral, and to the right sino-spiral.

Thus at the base, bulbo-spiral fibres are anterior, sino-spiral posterior (fig. 2); in the middle third, bulbo-spiral are on the left margin, sino-spiral on the right (fig. 3); while at the apex, bulbo-spiral form the posterior horn, and sino-spiral the anterior horn of the vortex.

To this general statement, some additions should be made, such as the circular fibres of the conus, and the longitudinal fibres in the posterior interventricular sulcus, but these will be dealt with fully under the heading of variations. Also, in some hearts, a band of superficial sino-spiral fibres is seen passing across between the apices from the posterior to the anterior surface, and, in others, a flat triangular surface is left at the apex; these also will be considered under variations.

(ii) *Middle Layer.* In order to arrive at the deeper layers, these superficial fibres have to be reflected. The principle adopted here has been to make an incision across the middle part of the muscle, and reflect it towards its origin or insertion. The depth of the incision is arbitrary, and indeed varies with the condition of the heart muscle, whether systolic or diastolic. In the case of the superficial bulbo-spiral muscle, it is best made on the left margin at right angles to the direction of the fibres (fig. 3); in the case of the superficial sino-spiral it can be made in two places, on the posterior surface or on the anterior surface of the right ventricle (fig. 3). Sometimes, when a strong band of sino-spiral fibres goes between the two apices, both incisions have to be made or some fibres will be missed.

The upper fibres reflected up to the origins can be removed, cutting the fibres short to mark this area. The lower ones are kept in bands (which, if the fibres are thin, is a difficult matter); these bands are cut off short and noted for further use at a later stage in the dissection (figs. 4 and 5). Some difficulty may be met with at the right margin, especially if the incision is made too deep, when part of the deep sino-spiral muscle is reflected as in fig. 10. Also in this situation, especially in hearts taken from cadavers, there is a sharp edge of soft fat and muscle fibre which usually breaks off short. At the apex the reflection usually is easily made, and leaves a neat clean fibre surface.

We now come to the deeper fibres, i.e. fibres of the middle layer of the heart. These also have similar names, deep sino-spiral of the right ventricle, deep bulbo-spiral of the left ventricle. As soon as the superficial fibres are removed, a view of part of these fibres is obtained on the posterior surface of the left ventricle (fig. 5). The deep bulbo-spiral muscle has a definite lower edge well shown in the figure. The muscle itself is covered by the deep sino-spiral bundle near the base of the posterior surface of the left ventricle, and also for about half the length of the ventricle in the posterior interventricular sulcus. On the anterior surface of the left ventricle, the definite lower edge of the deep bulbo-spiral muscle is not so marked, as the separation between superficial and deep fibres is not easily made (fig. 4).

The next procedure is to make an incision in the deep sino-spiral fibres, once centimetre to the right of the posterior interventricular sulcus (MacCallum, 1900). This is done in this situation owing to the crescentic shape of the right ventricle, and because the external appearances posteriorly are deceptive. This incision is shown in fig. 5, and marks the beginning of the split into the septum, and the unrolling of the left ventricle, as originally done by

MacCallum. The split is continued, superiorly at first, by careful dissection with the blunt edge of the scalpel, special care being necessary in the upper and middle parts of the septum, owing to the thinness of the layer which belongs to the right ventricle. When the separation reaches the level of the angle

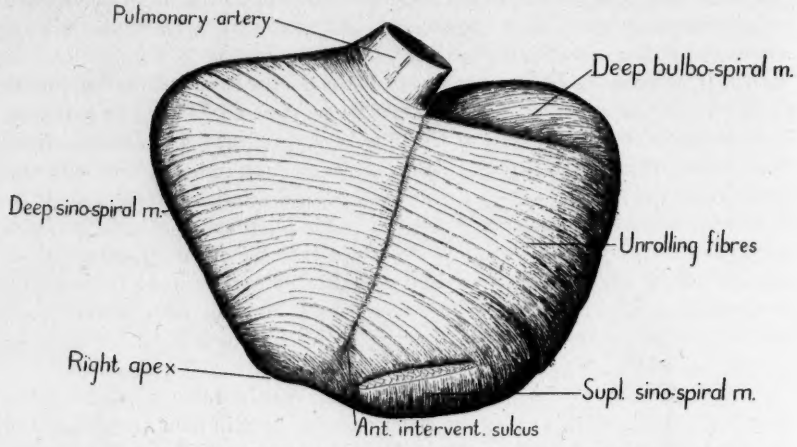



**Fig. 4. Anterior surface of dilated heart after reflection of the superficial layer of fibres.**

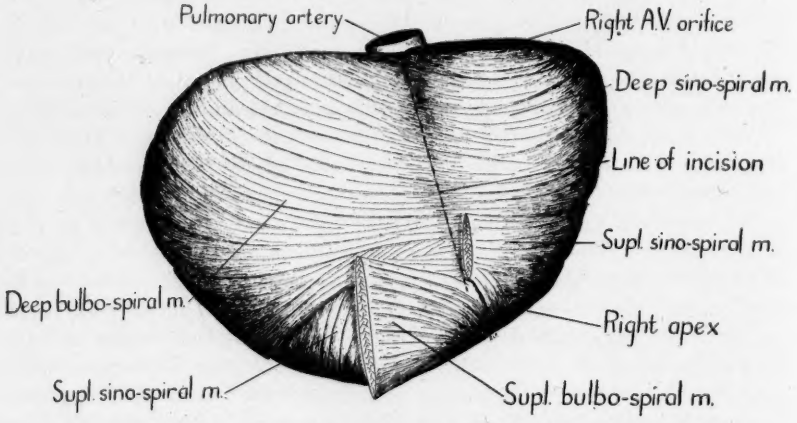



**Fig. 5. Posterior surface of dilated heart after reflection of the superficial layer of fibres.**

between the aorta and the left auriculo-ventricular orifice, some fibres are encountered coming from the region of the aorta in the left ventricle, passing to the right ventricle, and running down with its own fibres towards the apex. This muscle is the longitudinal muscle of the right ventricle (L.R.V. of Mall,

1911) (fig. 6). The origin of this muscle has in this investigation been found to be more extensive than that given to it by Mall. Instead of a small band of fibres attached to the base of the aorta, it is found to be attached along the left auriculo-ventricular ring and to be fairly extensive in width, covering over the pars membranacea septi. This gives a reinforcement to that part of the septum which belongs to the right ventricle, which is thin, and which has several foramina opening into its cavity (fig. 8). In a few hearts another muscle has been noticed, as in fig. 8, running also from the base of the aorta to the tendon of the conus, and this bundle has to be divided before further splitting can be carried out. This muscle will be discussed more fully under variations, but it must be mentioned here that it may be given the name of aortic muscle, and

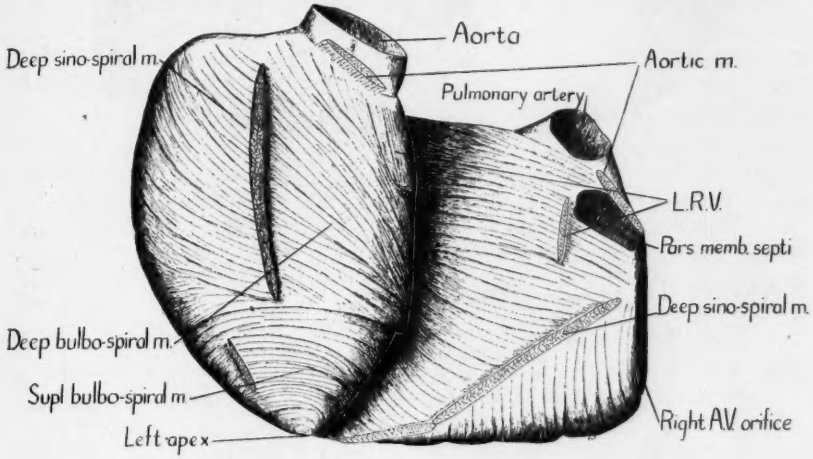



**Fig. 6. Early stage of unrolling of the left ventricle. Aortic muscle and longitudinal muscle of the right ventricle severed.**

that sometimes, not only does it become inserted into the tendon of the conus, but also its superficial fibres may run over the tendon to be continuous with the superficial sino-spiral fibres (fig. 6).

Besides these two definite bundles of fibres connecting the ventricles, there are at the junction of the lower and middle thirds of the septum, a few fibres from the left ventricle interdigitating with those of the right ventricle. These are, however, so few and unimportant as not to merit a separate name. They seem to be just an intercommunication between bundles more marked than is the case elsewhere.

While the separation has gone further in the septum superiorly than it has down in the neighbourhood of the apex, after the division of these muscle fibres, the line the split takes can now be seen (figs. 5, 7, 12). It keeps definitely to the right of the cut end of the superficial bulbo-spiral fibres, and runs down

to the apex between these fibres and the triangular area of fibres running between the two apices of the ventricles. Also these superficial bulbo-spiral fibres can now be seen ascending in the septum underneath the deep bulbo-spiral muscle (fig. 7). The separation is continued superiorly and advances to

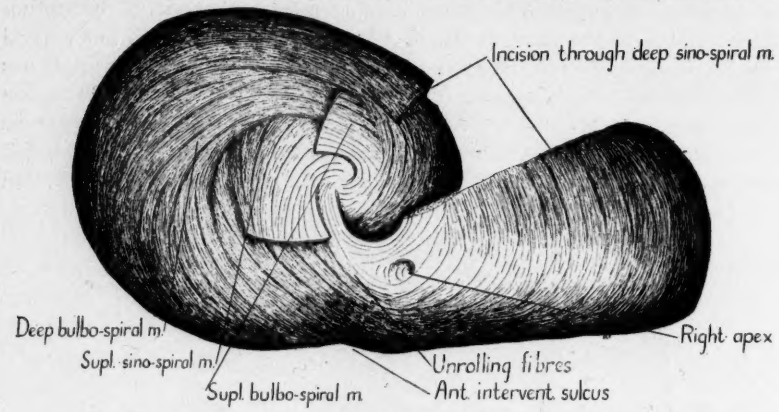



**Fig. 7. Apical view of heart in the same stage as in fig. 6, showing the three muscles entering at the apex.**

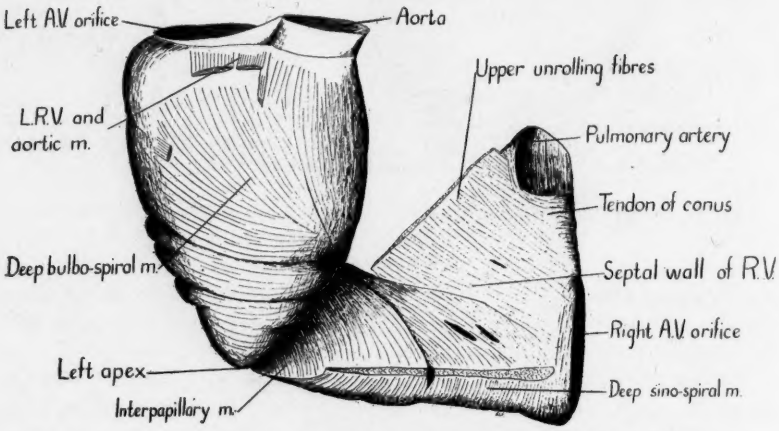



**Fig. 8. Further stage in unrolling the left ventricle, the upper unrolled fibres are now severed. Septal view of the deep bulbo-spiral muscle.**

the anterior interventricular sulcus, when the two ventricles are connected by deep sino-spiral fibres and the longitudinal muscle of the right ventricle anteriorly, and nearest the base; and by a thicker layer of fibres near the apex composed of interpapillary muscle (Gerdy, 1823; and MacCallum, 1900), and lower fibres of the deep sino-spiral band (fig. 6).

The upper unrolling fibres are all deep sino-spiral, and these are so thin and difficult to preserve that it is better to sever them (fig. 8), and trace them out before proceeding further.

As stated previously, they have an origin similar to that of the superficial sino-spiral band, i.e. from the posterior aspect of the left auriculo-ventricular ring and from the right auriculo-ventricular ring. They run round the right margin of the heart, the most posterior fibres passing obliquely towards the apex (figs. 4, 5), and then, after crossing the anterior interventricular sulcus, they begin to ascend again on the surface of the deep bulbo-spiral band. Here they have a variable course, usually reaching as far as the posterior surface of the left ventricle, and there fusing with the deep bulbo-spiral band. Sometimes this fusion does not occur until they reach the anterior part of the septum.

Having dealt with the upper division of the unrolling fibres, we can now unroll the left ventricle a little further. The unrolling is then blocked by the lower edge of the deep bulbo-spiral muscle, under which these fibres go (figs. 7, 8). At this stage also, the superficial sino-spiral muscle is just in front of these unrolling fibres, and it can be reflected a little further on to the left margin of the heart. It also goes under the lower edge of the deep bulbo-spiral muscle. At the posterior end of the septum the superficial bulbo-spiral band enters the left ventricle, and disappears under the lower edge of the deep bulbo-spiral muscle. Thus there are now three sets of fibres arriving at the apex of the left ventricle (as a matter of fact they *make* the apex of the left ventricle), and then, each goes under the deep bulbo-spiral muscle to form the deep layer of muscle fibres in the left ventricle (fig. 7).

To continue the analysis of the musculature of the left ventricle, we have to remove the deep bulbo-spiral muscle, but before this, a few facts about it must be made clear.

It is a circular muscle forming the middle layer of the left ventricle, and has been given different names by different writers, cylinder by Ludwig (1849), Triebwerk and basket by Krehl (1891). Mall (1911), however, calls attention to the fact that it is not closed below and basket as a term is not applicable. This muscle I have found to be attached round the left auriculo-ventricular ring on all sides except on the septal side of the aorta, where the longitudinal muscle of the right ventricle takes origin. This is more extensive than that given to it by Mall, who marks it out definitely, in a special figure (11), as being attached to the ring only in the region of the left margin. The fibres run from the origin downwards and from right to left on the anterior surface of the heart; the other fibres on its superficial surface are parallel to this line. In what is taken to be a normal heart, these fibres run to the junction of the lower and middle third of the length of the ventricle, and then reach the lower border of the muscle. Here they make an abrupt turn upwards, and become the deep fibres of the muscle running upwards to the left auriculo-ventricular ring, and in the general direction, obliquely from right to left on the anterior surface. This is shown exceedingly well in Mall's fig. 11. The fibres intermediate

between the deep and superficial surfaces of the muscle run more horizontally, in conformity with Ludwig's rule (1849), that any cube of the heart wall extending from the pericardium to the endocardium is composed of fibres which on the outside are at right angles to those on the inside. This, in fact, led Pettigrew (1864) to make three layers out of this muscle. This arrangement of loops explains very well the narrowing of the band of muscle seen in contracted hearts. In hearts boiled for two hours, as has been noted, the systolic state is assumed, and in these the deep bulbo-spiral muscle takes up, instead of two-thirds of the wall of the ventricle, only the upper third. Mall (1911) has noted also the difference in the size of this muscle in hypertrophied and dilated hearts. The importance of this muscle in the function of the heart as a pump will be discussed later.

(iii) *Deep Layer.* This again is divided into (*a*) fibres in the left ventricle, and (*b*) fibres in the right ventricle.

(*a*) The deep layer of fibres in the left ventricle can be divided, as has already been seen, into three bundles: (1) the unrolling fibres, composed of deep sino-spiral fibres, interpapillary muscles, and the longitudinal muscle of the right ventricle; (2) the superficial bulbo-spiral muscle; and (3) the superficial sino-spiral muscle. Each of these muscular bundles has several characteristics in common (fig. 7). They all run in the same direction, i.e. that which holds of nearly all fibres of the heart musculature, viz. from right to left across the anterior surface. They all pass under the lower edge of the deep bulbo-spiral muscle, and spread out in a fan-shaped manner; the lower fibres turning round sharply at the apex and forming the apex; the upper fibres usually going into a papillary muscle; while the middle fibres form the inner heart wall between the bulbo-spiral muscle and the endocardium. From this arrangement, and the oblique direction of the fibres, it follows that the upper fibres go into a papillary muscle of one surface, and then the middle fibres pass on up to the left auriculo-ventricular ring on the next surface in the usual order, i.e. from right to left on the anterior surface. This will be seen to hold good in the case of each of the three muscles. The apex also is composed of spiral fibres, which, as Pettigrew (1864) noted, is an arrangement to obtain for the apex, which is the weak part of the ventricular wall, great strength with comparatively little material.

1. The fibres which have been unrolled, and which come mainly from the right ventricle, pass under the deep bulbo-spiral muscle on the anterior surface (fig. 7). When this muscle is reflected, these fibres can be unrolled further, provided that the other two bundles, superficial sino-spiral and superficial bulbo-spiral, are unrolled simultaneously. The middle fibres from the right ventricle are then seen to pass upwards obliquely on the left margin (fig. 9). The upper fibres pass up vertically on the anterior surface to form, when they break away from the heart wall, the anterior papillary muscle; therefore, just at that site, it is possible for there to be a weak area in the heart wall (see later under Heart Rupture). At this situation also the cavity of the left ventricle

is opened, and the wall can be split almost to the apex obliquely in the line of the fibres. The middle fibres of this muscle pass round on the left margin, and are inserted into the left auriculo-ventricular ring on the posterior surface. The lower fibres, according to the rule, pass horizontally round at the apex in series with the apical fibres of the other two sets of deep muscles. At the anterior interventricular sulcus, there will be seen on the posterior surface of this muscle a small band of fibres which runs up from the apex (fig. 9). Its fibres are continuous with the transverse band between the apices (fig. 12), and at the anterior end of the septum the band runs upwards from right to left over the posterior surface of this muscle. This is called the interpapillary muscle, and forms part of the upper fibres which go to form the anterior papillary muscle.

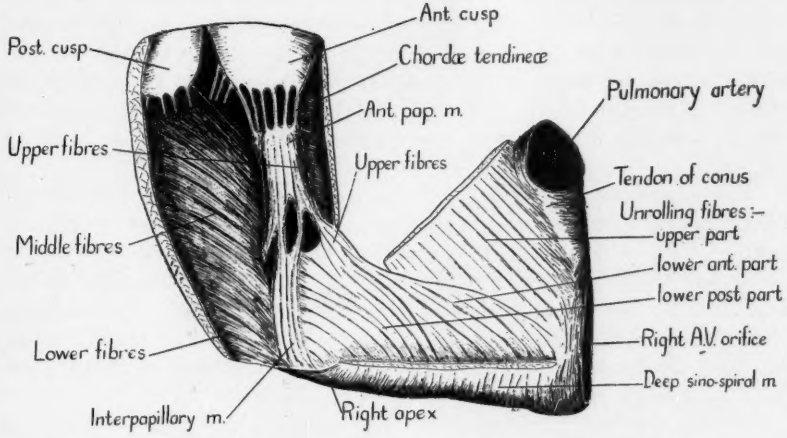



**Fig. 9. Interior of the left ventricle, after removal of endocardium and trabeculae carneae from the anterior surface.**

2. The superficial sino-spiral muscle forms the anterior horn of the vortex (fig. 3), and its upper fibres pass underneath the lower border of the deep bulbo-spiral muscle on the left margin (fig. 7). On the reflection of the deep bulbo-spiral muscle, this muscle can now be traced in the heart wall further round from the muscle just described. Its upper fibres, according to the rule, run upwards more vertically than the middle fibres to form the posterior papillary muscle, and hence reach their insertion, the left auriculo-ventricular ring. Just before these fibres pass from the heart wall to the posterior papillary muscle, the cavity of the left ventricle is opened and the split can be carried down to the apex in the direction of the fibres. During this splitting, however, the small trabeculae cordis or columnae carneae, which form intercommunicating bands, have to be severed. This split therefore separates the unrolling fibres from the superficial sino-spiral muscle. The middle fibres run more obliquely than do the upper fibres, and are inserted into the left auriculo-ventricular ring

further round than the unrolling fibres, i.e. on the septal surface. The lower fibres continue round the apex at a sharp curve for one third of a circle (fig. 7), and then ascend towards the base.

3. The superficial bulbo-spiral fibres form the posterior horn of the vortex (fig. 3), and then the upper fibres are seen to pass under the deep bulbo-spiral muscle at the posterior margin of the septum (fig. 7). The upper fibres ascend almost vertically in the septum to be attached to the auriculo-ventricular ring on this surface. They form the trabeculae cordis on the septal surface, and, when a small papillary muscle is situated on this surface (as it is in one-third of the cases), these fibres form that muscle. The middle fibres go round in the septum and are attached to the left auriculo-ventricular ring on the anterior surface. The lower fibres follow the rule and take up one-third of the apex. As with the other two muscles, this muscle on being gradually reflected, allows one to open into the cavity of the ventricle at the posterior margin of the septum, and this split also can be carried down to the apex. When these three splits are made the muscular wall of the left ventricle can then be spread out flat and the analysis of the muscle fibres made from the interior, as in Mall's fig. 18.

This arrangement of the muscle fibres largely follows from MacCallum's analysis of the foetal pig's heart; but, instead of any of these three layers being nearer the internal surface, as MacCallum (1900) states, they all three occupy some part of the internal surface by means of the overlapping which occurs (fig. 7). This also conforms with Pettigrew's statement (1864), when he notes the thinness of the apex, and that to give it the greatest strength possible the fibres are arranged in a spiral direction. The physiological application will be studied later.

(*b*) The deep layer of fibres in the right ventricle is, at present, hidden on the posterior and anterior surfaces by the deep sino-spiral muscle which forms a definite thick layer, especially on the posterior surface (fig. 5). This bundle gains attachment from the posterior aspect of the left auriculo-ventricular ring and from the posterior and right aspects of the right auriculo-ventricular ring. The fibres are almost horizontal in their course and can be easily reflected from the posterior surface of the right ventricle, but on the right margin of the heart the cavity of the ventricle appears (fig. 10). The deep fibres here ascend obliquely to their insertion, the right auriculo-ventricular ring, while the superficial ones pass round the anterior surface to become part of the unrolling fibres, especially the upper division.

Those deep sino-spiral fibres which take origin from the right side of the auriculo-ventricular ring do not take up this course, but form the muscle fibres on the superior surface of the conus arteriosus. There the lower fibres pass to the anterior aspect of the pulmonary artery, and the upper ones to the aortic aspect (fig. 10, and schema 21). These fibres take some part in forming the channel on the inner surface of the ventricle on contraction (fig. 2). This condition is comparable to that demonstrated in the heart of the bird by Pettigrew

(1864) (see later under Function). The unrolling fibres make up some of the deep layer of the right ventricle, and these will now be described.

1. The upper group of unrolling fibres is very thin, and is made up of fibres from two sources, fibres from the outer side of the right ventricle, i.e. deep sino-spiral fibres, and fibres from the tendon of the conus running down in the septum. These two sets join at an acute angle in the anterior interventricular sulcus, the angle being rounded off by perforating fibres of the superficial sino-spiral band (fig. 15, and schema 22). These would account for the fibres mentioned by Mall (1912) in his account of the development of the

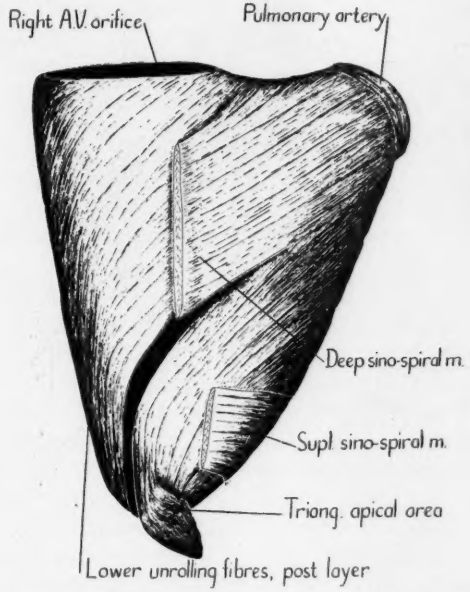



**Fig. 10. Lateral view of right ventricle, showing the opening into its cavity under the deep sino-spiral muscle.**

musculature of the heart, where he names fibres having this course as the longitudinal muscle of the right ventricle; this muscle, however, tends to join the unrolling fibres. These fibres may be compared with the perforating fibres noted by Pettigrew in his description of the ventricle of the fish and the reptile (1864, p. 446). In these animals the deeper layers of the heart wall are characterised by the presence of a large number of perforating fibres. In some of my specimens these fibres have actually formed a definite bundle passing inwards near the apex at the anterior interventricular sulcus (fig. 15) (see later under Variations).

2. The lower group of unrolling fibres is a much more definite bundle

(figs. 8 and 9), very strong, and can be divided into two layers: (1) an anterior layer which ascends over the septum of the right ventricle to the posterior part of the right auriculo-ventricular ring; (2) a posterior layer which constitutes the main part of the muscle, and which at its lower end joins the triangular area between the two apices (fig. 10). This posterior layer reaches the apex of the right ventricle, and then abruptly turns up in the posterior surface, part of it forming the posterior papillary muscle. Its fibres gain attachment to the right auriculo-ventricular ring on the right margin and on the anterior surface, and in some specimens extend forward to the conus round the auriculo-ventricular ring.

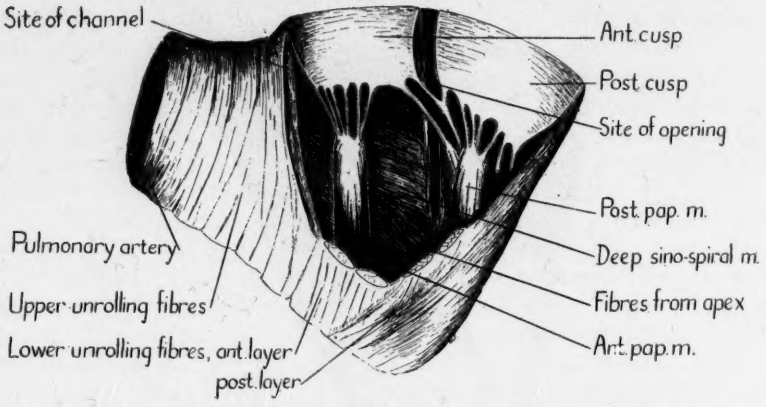



Fig. 11. Interior of the right ventricle after cutting away the septal wall, showing the anterior and posterior papillary muscles and the composition of the anterior wall.

3. The fibres from the triangular area at the apex (fig. 10) pass round, ascending in the anterior wall, and then, on reflecting this muscle, the cavity of the right ventricle is opened. Separating this opening from that caused by the reflection of the anterior unrolled fibres is the insertion of some of the deep sino-spiral fibres, which take some part in causing the concavity seen on contraction (fig. 13). The openings made here are now carried down to the apex, and one of them also through the auriculo-ventricular ring, and then the papillary muscles can be demonstrated (fig. 11).

The papillary muscles of the right ventricle, if not three in number, can be grouped under three headings: (*a*) the papillary muscle of the posterior wall receives its fibres mainly from the posterior layer of the lower unrolling fibres; (*b*) the anterior papillary muscle from the fibres of the apical triangle, and thus these fibres are called the interpapillary muscle (Mall, 1911); and (*c*) the small septal muscle or group of muscles from the lower unrolling fibres. Under this head we may consider the supraventricular crest or eperon of Wolff (1780), which can be seen on the inner aspect of the conus. This, in the contracted

heart, is seen to be continuous with the fibres forming the groove on the superior aspect of the base.

The action of these various muscle fibres will be discussed under Physiology.

### *Variations*

In the dissections made of the musculature of the ventricles, a number of variations were seen, and these can be classified according to the layers in which they occur.

1. *Superficial Layer.* In this layer we may notice first the varying number of fibres round the conus (figs. 4 and 10). Mall (1911) was inclined to believe there are no circular fibres round the conus. In this investigation, this was found to be the case in contracted hearts; but in hearts not boiled definite circular fibres were found and are shown in figs. 10 and 11. It is therefore supposed that in contraction they descend underneath the superficial ones.

In the literature I find no mention made of any fibres ascending obliquely on the anterior surface of the right ventricle, such fibres have, however, appeared in half the number of hearts dissected. These fibres run from the margo acutus upwards and to the left over the superficial sino-spiral fibres. They appear to be an offshoot from the main bundle of fibres on the diaphragmatic surface of the heart. They also cover over the area on the anterior surface of the right ventricle which becomes a concavity anteriorly in systole.

In connection with the superficial sino-spiral muscle, I have noticed that normally some fibres leave the deep surface of the muscle at the anterior interventricular sulcus, in an attempt to form a rounded anterior end to the cavity of the right ventricle. In a few cases a definite bundle of fibres, usually the lower sino-spiral fibres, has been observed to break off in this manner.

Also the arrangement of fibres at the apex of the heart, which has been described in various similes by different authors, appears to vary considerably, and the following types have been observed: (1) The vortex type in which the superficial fibres all appear to run to the apex of the left ventricle (fig. 13); in which case the apex of the right ventricle is not evident superficially, and is formed by deeper fibres of the superficial sino-spiral bundle; (2) A type in which some of the lower superficial sino-spiral fibres, on reaching the posterior interventricular sulcus close to the apex (fig. 3), pass over in an S-shaped manner between the apices of the ventricles to fuse with the superficial bulbo-spiral fibres, i.e. the posterior horn of the apex; (3) A variety in which there are a few fibres running directly transversely between the two apices (fig. 12); (4) A type where a triangular area is left between the two main superficial muscles at the apex, and in this area is situated the apex of the right ventricle (fig. 15).

Another variation, primarily described by Wolff (1780), consists in some of the sino-spiral fibres running vertically downwards in the posterior interventricular sulcus. This is mentioned also by Mall (1911), Sappey (1869), Meckel (1832), and Horner (1851). When these occur, the splitting into the

septum is made much more easily, as then a small incision only need be made through the transverse fibres near the base, and the remainder of the split can be carried down to the apex in the direction of the fibres.

2. ***Middle Layer.*** In this layer the deep bulbo-spiral muscle has been noticed, according as the heart is dilated or contracted, to vary, not only in the constriction of the ventricular cavity, but also in the length of the heart wall which it occupies. In the contracted heart it occupies the upper one-third of the wall, i.e. nearest the auriculo-ventricular orifice; while in the dilated heart this muscle is spread over twice that area, i.e. the two-thirds nearest the auriculo-ventricular orifice. This fact seems to be explained by the direction of the

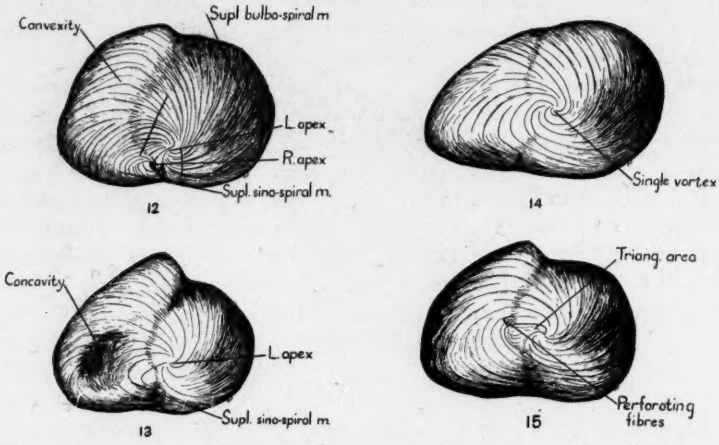



Fig. 12. Apical view of heart boiled after packing with cotton-wool; shows some sino-spiral fibres going in at the right apex.

Fig. 13. Apical view of a heart boiled with no packing; shows a concavity in the situation of the convexity in fig. 12; also some ascending fibres are present in this region.

Fig. 14. Heart showing a vortex composed of only left ventricle.

Fig. 15. Heart showing a triangular area between the left and right apices, and also some superficial sino-spiral fibres passing inwards at the anterior interventricular sulcus.

fibres on its inner and outer surfaces. These run respectively downwards and upwards in an oblique manner in the same direction, i.e. from left to right on the anterior surface.

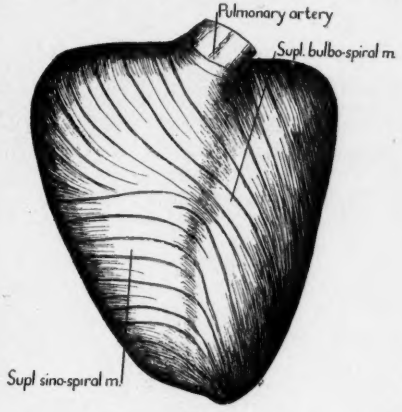
Also Mall (1911) especially stresses the fact that the deep bulbo-spiral muscle is attached to the left auriculo-ventricular ring only at the margo obtusus over a relatively short area; in my observations this attachment has not been definite, but has extended from one of that size to one in which the only part of the ring where the muscle gains no attachment corresponds to the aortic area and membranous septum.

The aortic muscle has shown one definite variation, in which some fibres ran from the base of the aorta over the tendon of the conus, and fused with

the fibres of the superficial bulbo-spiral muscle. This was quite plain, and was not due to any incorrect separation of the aorta from the conus (fig. 6).

Then in connection with the longitudinal muscle of the right ventricle; this has been noted to come from the left auriculo-ventricular ring (fig. 8) as well as from the base of the aorta, as described by Mall (1911).

The deep sino-spiral muscle has been noticed to vary in the same manner as the corresponding bulbo-spiral muscle, according as to whether the heart is in the systolic or diastolic state. Thus in systole it takes up the upper one-third of the heart wall, while in diastole it occupies the upper two-thirds. The importance of this in the action of the heart will be discussed later.

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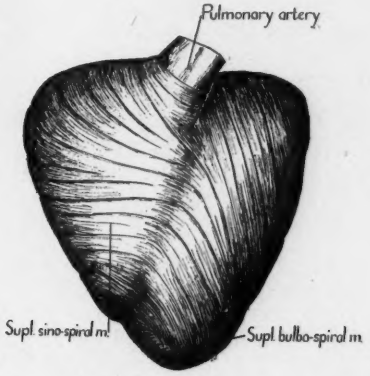


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Fig. 16. Anterior view of a foetal heart treated with 3 per cent. carbolic acid.

Fig. 17. The same heart as in fig. 16 after boiling; shows increased demarcation of the right and left vortices, and also the appearance of superficial bulbo-spiral fibres on the anterior surface of the left apex.

3. *Deep Layer.* Any variations in the deeper layers of the heart wall are difficult to determine, owing to the fact that the actual bundles can be dissected with any degree of certainty only within wide limits. Therefore, of the deep layer of muscles in the left ventricle, the arrangement is so varied that the one given can be taken only as an average. In the right ventricle the arrangement is more definite, but the presence of larger trabeculae carneae render separation so difficult that the muscles cannot be unrolled and laid out flat as with the left ventricle.

### *Summary of the Musculature of the Ventricles*

#### *Superficial Layer*

1. Superficial bulbo-spiral muscle arises from the tendon of the conus and anterior part of the left auriculo-ventricular ring. It passes almost vertically down the anterior surface and left margin with a slight twist to the left, and so enters the apex

on the posterior surface of the left ventricle to form the posterior horn. Here it is gathered into a narrow but thick bundle.

2. Superficial sino-spiral muscle arises from the posterior part of the left and from the whole of the right auriculo-ventricular ring. It courses horizontally round the posterior surface of both ventricles, and then over the anterior surface of the right ventricle, and is inserted at the apex on the anterior surface of the left ventricle. It forms the anterior horn of the vortex, and is wider than the posterior but not as deep.

### *Middle Layer*

1. Deep bulbo-spiral muscle is demonstrated after splitting into the septum and unrolling the left ventricle from the right as far as the anterior end of the septum. Then if the upper unrolling fibres are severed, this muscle is clearly shown. It arises from the left auriculo-ventricular ring and aortic orifice except in the region of the septum. It is a circular muscle cylindrical in shape, and makes up the thickness of the left ventricular wall for the upper two-thirds in the diastolic state. Its fibres on the outer surface run downwards and forwards in the septum, and to the left on the anterior surface, and on reaching the lower border turn upwards, following the same direction on the inner surface of the muscle to be inserted in the left auriculo-ventricular ring.

2. Deep sino-spiral muscle arises from the posterior aspect of the left auriculo-ventricular ring and from the right auriculo-ventricular ring. Its fibres form a band occupying at the posterior interventricular sulcus the upper two-thirds of the heart wall, and usually about 0·8 cm. in depth. They run horizontally round the posterior surface. Some deep fibres pass in on the anterior surface of the right ventricle, while the superficial fibres pass round to form part of the unrolling fibres going to the anterior aspect of the left ventricle.

3. Aortic muscle and the longitudinal muscle of the right ventricle may be added to the muscles of this layer also. The latter, however, is included in the musculature of the deep layer of the left ventricle.

### *Deep Layer*

(*a*) *Left ventricle.*

1. Unrolling fibres arise from three sources: (i) deep sino-spiral muscle; (ii) longitudinal muscle of the right ventricle; and (iii) interpapillary muscle. They may be divided into two groups, upper and lower. The upper is thin and is composed of deep sino-spiral fibres, while the lower is composed of all three muscles, and follows the usual distribution in three divisions; the upper fibres with the interpapillary muscle form the anterior papillary muscle; the middle fibres pass round to the posterior surface of the left auriculo-ventricular ring; while the lower fibres take up one-third of the apex.

2. Superficial sino-spiral muscle forms the anterior horn of the vortex, and now passes upwards under the lower border of the deep bulbo-spiral muscle to be distributed in three groups; the upper fibres form the posterior papillary muscle; the middle fibres are inserted into the left auriculo-ventricular ring on the septal surface; while the lower fibres take up the usual third of the apex.

3. Superficial bulbo-spiral muscle forms the posterior horn of the vortex, and from there it passes under the lower border of the deep bulbo-spiral muscle at the posterior margin of the septum. The upper fibres form the trabeculae cordis on the septal surface, and when a small papillary muscle is present, its fibres pass into that muscle. The middle fibres pass up to the left auriculo-ventricular ring on the anterior surface. The lower fibres continue round at the apex.

(*b*) *Right ventricle.*

1. Unrolling fibres form part of the deep layer of the right ventricle, and are divided into two groups, upper and lower: (i) The upper fibres come from two surfaces, the septal surface and the anterior surface, the fibres from the latter being deep sino-spiral fibres; (ii) The lower fibres are composed of the anterior and posterior sets, the anterior ascending in the septum of the right ventricle to the posterior part of the right auriculo-ventricular ring, while the posterior set reach the apex of the right ventricle and turn upwards in the posterior wall. Here they give off fibres to the posterior papillary muscle, and finally are attached to the right auriculo-ventricular ring on the right margin and anterior surface.

2. Fibres from the triangular area at the apex, which are also called the inter-papillary muscle, ascend in the anterior wall obliquely to the anterior part of the right auriculo-ventricular ring and also the conus.

3. Deep sino-spiral muscle, besides making up the middle layer of the right ventricle, sends fibres into the deep layer. These are (i) the perforating fibres at the anterior interventricular sulcus. (These also may come from the superficial sino-spiral muscle.) (ii) Fibres of the deep sino-spiral muscle which at the right margin emerge from its deep surface and form some part of the deep layer.

4. The papillary muscles are formed as follows: (i) The posterior papillary muscle by fibres from the posterior layer of the lower unrolling fibres; (ii) The anterior papillary muscle by fibres from the apical triangle, i.e. the interpapillary muscle; (iii) The small septal muscle from the lower unrolling fibres.

## *Spontaneous Rupture of the Heart*

*Introduction and Literature.* During the study of the musculature of the ventricles, the varying depth of the muscular layer in different situations suggested that this fact might have some bearing on heart rupture. As has already been mentioned, the apex of the left ventricle is so thin that some of the older writers thought it had no muscle fibres at all (Stensen, 1630). The literature has been investigated from this point of view, and the results are here briefly given.

It was formerly thought that spontaneous rupture of the heart was due to a sudden strain acting on a thin piece of normal heart musculature. Todd (1836) and J. Cruveilhier (1830) both expressed this opinion, and also stated that the most common region affected is the apex of the left ventricle. They explain this as being due to the thinness of the apical musculature. Cruveilhier gives as his authorities Rostan and Laennec, and indeed states that those ruptures which occur in places other than the apex are usually traceable by means of a probe downwards under the subepicardial fat to an internal opening at the apex.

In 1872, however, Quain gave an analysis of 100 cases, in which 76 per cent. of the ruptures are situated in the anterior wall of the left ventricle. His explanation of this is that most of the hearts examined were in the state of fatty degeneration, and that usually a sudden strain causes rupture of the heart wall at that point. He also gives aneurism of the heart as a cause of cardiac rupture, and half of these occur at the apex, due, according to Rokitansky, to the liability of this part of the heart to chronic myocarditis.

Of the textbooks, MacCallum (1919) suggests the formation of an anaemic infarction in the heart wall causing the weak area. Muir (1924) suggests three causes, or at least mentions cardiac rupture under these heads: (1) fatty infiltration, but this is most marked in the right ventricle, and most ruptures occur in the left ventricle; (2) acute suppurative myocarditis causing rupture, especially in staphylococcal infections; and (3) aneurismal dilatation between the columnae carneae.

In 1925 Krumbhaar and Crowell contribute an article on heart rupture based on all the reported cases, i.e. about 600 in all. They put the most frequent site of rupture in the anterior wall of the left ventricle, then next frequent in the posterior wall, and then at the apex. The anterior wall is most often affected, owing to the fact that the descending branch of the left coronary artery is the one most markedly atheromatous. This is, in their opinion, the cause of the rupture, owing to thrombosis of the vessel leading either to actual infarct of the wall, or to a poor state of nutrition of the wall, and then this going on to cardiac aneurism. Thus a weakened area is produced in the heart wall. Their results oppose the factor of heightened pressure inside the ventricle, i.e. sudden exertion, because in half the cases rupture occurs during sleep. They have noted that "not infrequently the internal opening is found hidden behind a papillary muscle, where it would seem to be relatively well protected." This situation, however, from this investigation of the general musculature, appears not to be as strong as the rest of the heart wall, since some of the neighbouring fibres coming up from the apex become concentrated to pass into a papillary muscle.

The latest work on this subject, by Nuzum and Hagen in 1926, refers also to the anterior wall as the favourite site of rupture, and makes no mention of the apex of the heart.

From these writings it appears that the earlier works are not correct in the situation of the rupture, but that it most frequently occurs in the anterior wall on the left ventricle, close to the septum, and usually with its internal opening hidden by a papillary muscle. The selection of that site for the rupture is due more to vascular changes in the heart wall than to any inherent weakness in its musculature.

### *Pathological Findings*

These have been obtained from four hitherto unreported cases of which the specimens are in the pathological museum of the Otago University Medical School. No details of clinical history were available, and so only the naked eye and microscopical appearances are given.

#### *Specimen I. T.* 70

*Macroscopical Appearances.* Halfway down the anterior wall of the left ventricle, near the septum, there is a horizontal rupture, 2 cm. long, running in the direction of the superficial fibres (fig. 19). The line the rupture takes through the heart wall slopes downwards towards the apex, the line of the internal orifice being parallel to

that of the external orifice, and its situation about 2 cm. from the apex. The wall of the heart is pale with an irregular pink zone as from infarction, which extends into the anterior papillary muscle, especially on its inner surface.

The coronary arteries are slightly atheromatous, but atheroma and sclerosis are well marked at the openings of the coronary arteries in the sinuses of Valsalva. The general appearance in the aorta is that of a syphilitic aortitis.

*Microscopical Appearances.* The heart wall is in a state of chronic interstitial myocarditis with fibrosis and atrophy of heart muscle with hypertrophy of adjacent fibres. There is no suggestion of recent infarction.

The descending branch of the left coronary artery shows marked thickening and sclerosis.

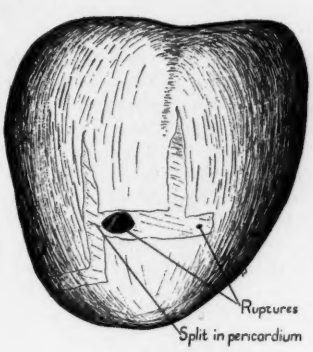


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Fig. 18. Specimen of heart rupture on the posterior wall of the left ventricle, with separation of muscle fibres and splitting of the pericardium.

Fig. 19. Specimen of heart rupture on the anterior surface of the left ventricle.

### *Specimen II. T.* 65

*Macroscopical Appearances.* The rupture in this case is a vertical one situated in exactly the same place as the preceding. It is due to an infarction leading to the formation of a fairly acute aneurism. The infarction extends over the lower half of the anterior wall of the left ventricle including the apex; it affects mainly the inner surface, and leaves a rim of muscle surviving around its circumference, a fairly common appearance in infarction.

The coronary arteries are narrowed and atheromatous, while the aorta is relatively free from atheroma.

*Microscopical Appearances.* This shows recent infarction with necrosis of muscle fibres, small haemorrhages scattered throughout the infarcted area, and marked leucocytic infiltration, especially of a polymorphonuclear character.

The descending branch of the left coronary artery is generally calcareous, and at one spot is closed by a thrombus.

### *Specimen III. T.* 32

*Macroscopical Appearances.* The rupture is in the same site as the preceding, and is horizontal as in the first specimen, parallel with the vessels and superficial muscle fibres. The internal orifice is slightly higher than the external, and so this rupture at any rate cannot be taken as coming from the direction of the apex.

The coronary arteries are narrowed and sclerosed, and the site of rupture is surrounded by a small area of infarction. The appearance of the aorta suggests syphilitic aortitis.

*Microscopical Appearances.* These are those of a recent infarction with necrosis of muscle fibres, infiltration of inflammatory cells, and haemorrhages between the dead fibres. Leucocytes are mainly polymorphonuclear in type. Some hypertrophied muscle fibres are present, and suggest the presence of a degree of chronic interstitial myocarditis previous to this infarction. A large amount of haemorrhage is situated at the edge of the rupture, and this may partly account for the choice of the site of rupture, i.e. the formation of a haematoma.

The coronary artery is sclerosed, and shows intimal thickening.

### *Specimen IV. T.* 6

*Macroscopical Appearances.* The site of rupture in this case was on the posterior aspect of the left ventricle (fig. 18), at the junction of the middle and lower thirds in the middle of the posterior surface. It occurs as a small round hole, one centimetre in diameter, through a thin layer of muscle. Radiating from this there are three tears in the pericardium and superficial muscle fibres, one running up towards the left auricular appendix, one going up the posterior interventricular sulcus, and one passing round the left margin of the heart. From the appearance of these tears, it is difficult to state whether they were produced ante-mortem or not. The muscle wall is thin and friable, due to the formation of an aneurism of the lower posterior wall and apex, from old infarction. Internal examination shows a split through the septal wall of the left ventricle at the posterior interventricular sulcus. This passes round the right ventricular wall in the vertical plane and in the line of the fibres to a second rupture (fig. 18).

The left coronary artery has a definitely calcareous wall.

*Microscopical Appearances.* These are cloudy and suggest the possibility of some autolysis having occurred before preserving the specimen. The muscle fibres in the thinned area appear as good as those elsewhere, and no obvious fibrosis is seen in the muscle. Thus the general microscopical appearance does not suggest infarction. There is, however, a distinct fibrous thickening of the subepicardial layer through which the tear is situated.

The coronary artery shows a diffuse sclerosis.

## *Conclusions*

The first three cases are in line with the results of Krumbhaar and Crowell (1925), both as regards etiology and site of rupture; two from recent infarction (*T.* 65 and *T.* 32), and one from old infarction (*T.* 70).

No definite conclusion can be drawn from the last case, owing to the autolysed appearance of the sections of muscle fibres. Naked eye examination suggests aneurism from old infarction, while microscopically there is no fibrosis to support this. There is, however, some subepicardial fibrosis around the area of tearing, and this, with the thinness of the heart wall in this region, suggests aneurism as the most likely explanation.

As regards the site of rupture, the anterior wall at the junction of the middle and lower thirds is the most common, and here the descending branch of the left coronary artery is affected. The line of rupture is parallel with the superficial muscle fibres, but cuts directly across some of the deeper ones. Two of the three appeared to have the internal opening underneath a papillary muscle.

One (*T.* 32) had its internal orifice a slight distance separated from the base of the papillary muscle. Under this head it may be mentioned that a case recently reported (Saphir, 1927) shows rupture in this situation also, i.e. on the anterior surface and left margin. This was due to indirect trauma in a child, involved in an automobile accident, the greatest force being exerted in the region of the right pelvis.

In conclusion the choice of site of rupture appears to depend on: (1) the area of infarction, i.e. which artery is concerned; (2) the presence of any large amount of haemorrhage in that area; and sometimes (3) the weakness of the heart wall just above the point of emergence of a papillary muscle[1].

## *B.* Auricles

The first good account of the musculature of the auricles was given, in 1876, by Henle, who described the various fibres in great detail. The study is not taken up again until, in 1907, Keith gives a description, and also Lewis in 1917, but both these observers conducted their investigations more from the point of view of function than for the bare anatomical details. These are finally made clear in 1920 by Papez, whose description I have followed in my preparations. He, however, makes special names for many of the muscle bundles.

The earlier writers, Gerdy (1823), Luschka (1860), and Henle (1876), have noted the division of the fibres into external and internal layers, the external being mainly transverse, the internal mainly longitudinal. They do not make it clear that, posteriorly at any rate, there are very few connecting fibres between the two auricles.

The arrangement of the muscle fibres of the auricles can be investigated from two aspects; the external by peeling off the pericardium, and the internal by peeling off the endocardium. This can be greatly assisted by splitting into the auricular septum posteriorly, in a manner similar to that of MacCallum (1900) for the ventricles. In the auricles, however, it can be much more easily performed, owing to the fact that posteriorly there are very few connecting fibres between the two auricles.

This procedure is better carried out in a "carbolic" heart with the auricles distended. Holding the left auricle in the left hand, the operator gently separates the right auricle from the left with the handle of a scalpel. This is continued as far as the fossa ovalis, and then here the narrow point of the scalpel must be used to separate off the endocardium (fig. 20), which is all the septum that belongs to the right auricle in this area. This separation may then be carried on to the anterior end of the septum, until the auricles are connected only by

[1] After the above had been written, my attention was drawn to an article by Goodall and Weir (1927), an analysis of 18 cases of rupture of the heart. In all their cases the coronary arteries showed marked arteriosclerosis, i.e. calcification, and in 8 cases the site of the rupture was situated on the anterior surface of the left ventricle.

the fibres running between the anterior surfaces of each, i.e. especially the interauricular band. The musculature can thus be divided into that of (*a*) the left auricle, and (*b*) the right auricle.

(*a*) *The left auricle.*

The fibres here are divided into external and internal. The finer details are given by Papez (1920), and the following represents a brief statement of the main facts ascertained from my own dissections.

(1) The external fibres are easily traced by removing the pericardium, and, at first sight, appear to form a network, which in diastole is separated by a number of open triangular spaces, and which in systole comes together so that neighbouring fibres become almost parallel.

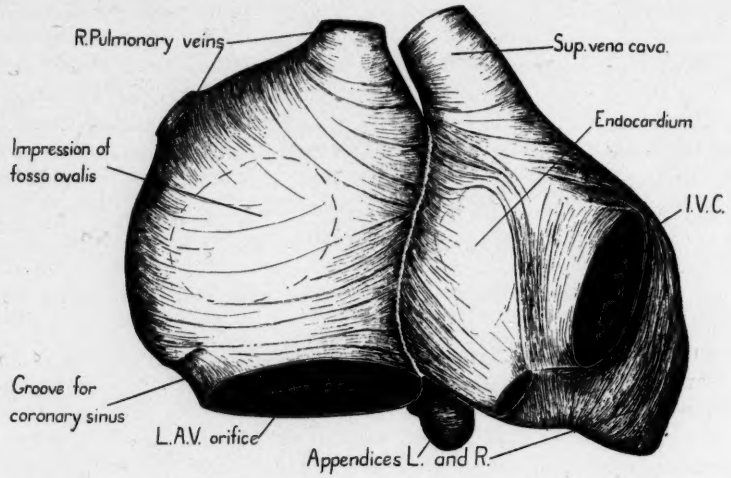



Fig. 20. Appearance of the auricular septum after splitting it from the posterior aspect.

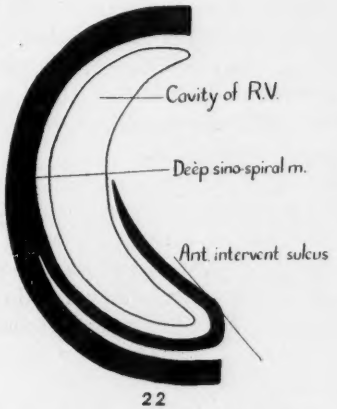
On the posterior surface in the area between the lower left pulmonary vein and the auriculo-ventricular ring, the fibres are transverse, and laterally these divide into two bundles which pass above and below the auricular appendix, each giving circular fibres to the appendix. Medially they spread out in a fan-shaped manner, the upper fibres fusing with the circular fibres round the lower pulmonary veins, the middle fibres running across the posterior surface into the septum, and the lower fibres turning down to form a vertical layer over the coronary sinus, and then going to the auriculo-ventricular ring. These on contraction have a sphincteric action on the coronary sinus.

Anteriorly these two bands, running above and below the auricular appendix, fuse to form a transverse bundle on the anterior surface. The bulk of these fibres pass into the interauricular band (interatrial band of Papez), running up to the sino-auricular region of Keith and Flack. The lower fibres

run down to the left auriculo-ventricular ring, and also to the bundle passing below the right auricular appendix. These help to straighten out the anterior concavity in contraction. The upper fibres fuse with the deeper layer, and run longitudinally over the superior aspect to the area between the pulmonary veins on the posterior surface, and thus fuse with the deeper longitudinal fibres.

The external layer in the septum contains fibres which run transversely forwards, and can be seen to concentrate on the interauricular band, from which they may be said to originate. On splitting the septum, on the left auricular side, there do not seem to be any longitudinal fibres. This relative thinness of the left auricular septum is in accordance with the development (His, Sen., 1886), and the splitting may be taken as indicating the separation into the original septum primum and septum secundum.

21




22

Fig. 21. Schematic figure of the upper division of the deep sino-spiral fibres, bifurcating to pass on either side of the pulmonary artery.

Fig. 22. Schematic figure of a horizontal section through the right ventricle, showing some fibres of the deep sino-spiral muscle perforating at the anterior interventricular sulcus.

The rest of the external fibres are made up from the fibres encircling the orifices of the pulmonary veins. These are seen best in a heart in the diastolic state, as in systole they form a curtain which is seen from the inner aspect of the left auricle, and which forms a groove on the posterior aspect at the junction of the pulmonary veins with the auricular wall. There are circular fibres round each vein, and also circular fibres round all four veins, and these latter, with the taenia terminalis sinistra, form this curtain in the interior of the auricle. The fibres forming the large circle may be taken to fuse laterally with the taenia terminalis sinistra, and medially with the internal layer of the septum, thus forming some of the transverse fibres in the septum. Papez (1920)

stresses this last fact by naming these circular fibres, the septo-pulmonary bundles[1].

(2) The internal layer can be seen on careful removal of the external layer, but is best demonstrated by peeling off the endocardium from the inner surface. These fibres are longitudinal in direction, forming a weak layer over the superior aspect of the auricle, and passing down to the anterior and posterior parts of the left auriculo-ventricular ring. In the appendix they form the musculi pectinati, and are concentrated in the taenia terminalis sinistra. This is divided by Papez into the left anterior and posterior crests, but from a functional point of view, is best considered as a whole. In these specimens, apart from fibres descending over the coronary sinus, no connection can be made by the left auricular musculature with that of the inferior vena cava.

(*b*) *The right auricle.*

(1) The external fibres of the right auricle are not as sharply marked off from the deep fibres as they are in the left auricle. Also the external fibres do not keep to the transverse direction.

There are two bundles which arrive on either side of the superior vena cava on the posterior surface. The lateral one comes from the interauricular band, and the medial one from the longitudinal fibres in the septum and also from the interauricular band.

The medial one forms most of the posterior wall of the auricle by radiating out in a fan-shaped manner; the most medial fibres pass to the inferior vena cava, and fuse with the few circular fibres it possesses (intercaval band of Papez). The central part of the bundle radiates to the posterior part of the right auriculo-ventricular ring, forming most of the posterior wall. The lateral part encircles the lower aspect of the appendix, forming there a definite bundle which runs round below the appendix just above the right auriculo-ventricular ring to the anterior surface. There these fibres pass mainly into the septum, the upper fibres encircling the appendix, the lower fibres going beneath the interauricular band into the septum.

The lateral bundle, i.e. the one nearest the sino-auricular node (Keith and Flack), is forced by the radiation of the medial bundle to go mainly over the posterior surface of the appendix, but its most medial fibres pass down under the radiating fibres above-mentioned, to the circular muscle of the inferior vena cava.

(2) The internal fibres are those of the taenia terminalis (His, Sen., 1886), and the musculi pectinati. The former run longitudinally from the auriculo-ventricular ring up to the superior aspect, and then down to the anterior surface, fibres not being so prominent as on the posterior surface. This group also Papez divides into anterior and posterior crests, but Keith (1902) considers the taenia as extending also on to the anterior surface. The fibres of the musculi pectinati have a transverse direction.

The septum of the right auricle is thick posteriorly and anteriorly, and thin

[1] The union of these fibres with the septum inferiorly was recognised by Keith in 1902.

over the fossa ovalis, where, on splitting the septum it is found to be composed of endocardium. Its anterior part is made up of some vertical fibres attached to the right auriculo-ventricular ring anterior to the inferior vena cava, and running up in the free edge of the limbus. Posteriorly they radiate out in the septum and posterior surface of the inferior vena cava, the lowest fibres turning down again to the right auriculo-ventricular ring. In this manner the fossa ovalis is formed[1]. Anteriorly the fibres are concentrated from the transverse fibres of the septum, and from the radiating fibres on the posterior surface. Papez (1920) has applied the name of septal raphé to this, and describes a free nerve-supply, i.e. to the left of the superior vena cava, while the sino-auricular node is to the right of this. He suggests that there may also be some pace-making function in the septal raphé, but that this has not been found by the electrocardiograph owing to its being difficult of access. On the other hand, he has not found any nodal tissue there, as suggested by Keith and Flack (1907).

The physiological application of this will be considered later.

## THE PHYSIOLOGICAL APPLICATION

Any enquiry into the function of these various muscle bands at once stops short when they are considered individually. The heart muscle contracts as a whole, and, though the musculature of the auricles and ventricles is separate, some of the muscle fibres of each have to be taken together to understand fully their action. This was pointed out by Keith (1907), and from his account is abstracted the idea of the two fulcra of the heart. Firstly, we consider the auricles and ventricles separately, and then secondly, group their actions together.

### 1. The Function of the Auricles

To understand this properly, we have first to obtain a fixed point or a fulcrum from which the muscle fibres can act. For the auricles this fulcrum, as has been pointed out by Keith (1907), can only be the venous mesocardium attached to the pericardial sac. This is in turn firmly bound to: (1) the roots of the lungs; (2) the diaphragm; and (3) the great vessels. When systole occurs, by means of the longitudinal fibres, shortening takes place, and the base of the then relaxing ventricle is pulled up towards the base of the heart, i.e. the fulcrum of the auricles.

Owing to the arrangement of the fibres, the shortening shows itself inside the right auricle by the taenia semicircularis bringing itself across the orifices mainly of the inferior vena cava, and partly of the superior vena cava. In this investigation the auricles were contracted by boiling, and it was then noticed that the taenia projected internally from the lateral wall half across these orifices. It thus can be considered as a valve, not a very efficient one certainly,

[1] On this, Keith (1902) bases his explanation of the course of the venous blood in the foetus.

but with the contraction of the circular muscle round the venae cavae, it will, to some extent, prevent any tendency to regurgitation[1].

A similar mechanism is present in the left auricle, and can also be demonstrated by boiling the auricles. Owing to there being no valves in the pulmonary veins (Poirier and Charpy, 1912), some means of preventing regurgitation into the ill-supported walls of the pulmonary capillaries must be provided. This is found in the circular muscle of each pulmonary vein, and this forms a type of sphincter to each vein. Also, around the four veins, there are circular fibres which run medially to the septum, and laterally to the taenia terminalis sinistra; and these fibres, in contraction, tend to form a muscular curtain hanging across the cavity of the auricle. This is not usually, however, as prominent as that in the right auricle. In some cases (Griffiths, 1903) a definite fibro-muscular band is present attached to the septal wall.

The result of this seems to be that, in systole, the part of the auricle which is developed from the primary auricle (His, Sen., 1886) attempts to shut itself off from the part developed from other structures. In the right auricle there is an attempt to form a sinus venosus, and in the left auricle to form a cavity which was formerly occupied by the original pulmonary vein.

Another observation on the contracting auricles can be explained along anatomical lines. It had been suspected that the part of the auricular wall around the orifices of the great veins contracted first, and this was even spoken of as preauricular contraction (Morison, 1913). The electrocardiographic experiments of Lewis (1917) confirm this, and now it can be demonstrated from the arrangement of the fibres. The sino-auricular node is situated on the right side of the superior vena cava; from this situation there is a small stream of fibres round the superior vena cava, and, in the intercaval bundle, down to the inferior vena cava. As soon as the contraction is inaugurated, these fibres are stimulated and contraction occurs, while, at the same time, the stimulus is conducted along them. When this reaches the left side of the superior vena cava, i.e. the septal raphé of Papez (1920), then the stimulus branches out in all directions and contraction occurs in the general auricular muscle. This, however, does not explain the free nerve-supply demonstrated by Papez to the left side of the superior vena cava.

### 2. The Function of the Ventricles

Here also a fulcrum must be laid down in order to understand the muscular action. Owing to the intimate connection of the two ventricles, the fulcrum will presumably act for both, but at first we will consider the left ventricle separately.

(*a*) *The left ventricle.* This fulcrum has been determined by Keith (1907) as the apex, though formerly Haycraft (1891) demonstrated, by means of needles fixed in the hearts of rabbits and cats, that on contraction there was

[1] Since writing the above, there has come under my notice the article written by Keith in 1902, and there these facts are also mentioned.

not much movement of the apex. At first sight this seems improbable from the anatomical appearance presented by the apex, lying freely, as it does, in the pericardial sac. But it has been determined that the base of the ventricles, i.e. the auricular base, moves down in systole towards the apex. And thus the apex of the left ventricle is taken as the fulcrum on which the muscle fibres act. Krehl (1891) also states there is no alteration in the longitudinal diameter. In opposition to this fact is the appearance of the deep bulbo-spiral muscle in a systolic heart. Instead of taking up two-thirds of the heart wall it occupies only one-third. Its fibres run mainly transversely with long obtuse-angled loops, and, if *it* should shrink so much, so there should be *à fortiori* a greater contraction of the longitudinal fibres of the muscles both deep and superficial to this one.

Keith (1907), in his explanation of the fixation of the apex, brought in the circular fibres as being antagonistic to the longitudinal fibres. I believe, however, that there is an alternative explanation, because, if the circular fibres shorten in the length of the ventricle, they cannot antagonise the longitudinal muscle. This aspect of the question will be discussed later, but, in the meantime, we may dispose of the question of the fixation of the apex. The deep longitudinal fibres contract, and tend to shorten the heart; the superficial ones, however, acting in a spiral direction, i.e. obliquely across the axis, cannot shorten the axis, because they are acting in a whorl. If the axis were to contract, the sides would bulge outwards, and this is shown not to be so. In fact, they contract inwards, but this, owing to the size of the heart wall, cannot be done to any appreciable extent, except just enough to come together to protect the apex. This formation of a concavity outwards is to be noted more prominently in the right ventricle. The findings of Lewis (1917) support these statements, when he notes the fact that the first appearance of contraction is above the apex. The fibres contract just above the apex, and then from the tension in the superficial fibres press in towards the centre. Then, when the few fibres that are present at the apex contract, they cannot perform any shortening of the axis, owing to the now solid wall they have to contract against. In this manner I believe that the apex becomes a fixed point, and brings the auricular base downwards by means of its inner longitudinal fibres, i.e. the papillary muscles, as Keith (1907) has pointed out, while the aortic base remains steady.

Having now arrived at the method for securing the apex, we next study in more detail the actual manner in which these longitudinal fibres react on the contents of the ventricle. The theory first laid down by Borelli (1681), is that upheld by Mall (1911) in a short note on the action of the heart. Borelli stated, "The true action of the muscle of the heart is the contraction of the ventricles, and the compression and expression of the blood contained in them is carried out after the manner of a winepress, and that, not by the contortion of the spiral fibres of the heart, but by their inflation and tension" (Foster, 1901). Mall adds to this the fact that the superficial fibres then straighten out in contraction, and cause the inner thickened fibres to curve upon themselves, and

wring the blood out of the heart. This is borne out by Pettigrew's description of the grooves becoming more spirally inclined in the casts of a contracted ventricle (1864). From this one might ask, why is it that the superficial fibres do not tend to unwind the deep musculature and papillary muscles? For one reason, that the deep fibres at the same time are being wound up and made more secure; and the other reason is explained by Lewis (1917). The contraction of the muscle fibres has been found by Lewis to occur on the inner surface before the external fibres, and so the inner loops are first tightened before the superficial fibres contract.

The longitudinal muscle now having been dealt with, it remains to dispose of the deep bulbo-spiral muscle. Here again Lewis states definitely that the fibres of the base contract later than the fibres nearer the apex. This may be applied to the action of the deep bulbo-spiral band, and thus the blood which has been wrung out of the lower third of the ventricle is sent up into the dilated aorta (Hesse, 1880; and Krehl, 1891) by a rapid type of peristaltic action of the deep bulbo-spiral band. In this action the muscle changes its position, from the upper two-thirds of the ventricular wall to the upper one-third. This action makes the expulsive movement of the heart complete, and, at the same time, also fulfils the other function which, I believe, can be ascribed to the deep bulbo-spiral muscle. It has been pointed out (Samways; Campbell, 1921) that the semilunar valves are not, structurally at any rate, competent to close the aortic orifice against the elastic recoil of the aortic wall, and that there thus must be another mechanism coming into action at the end of systole to support these. These writers thought it was probably some part of the heart muscle. The only part of the heart musculature which can possibly perform this function seems to be the deep bulbo-spiral muscle, and the fact that it contracts later than the other muscle fibres makes this hypothesis all the more likely. Also the type of contraction necessary to protect the valves is one in which the fibres project internally, and this is the only thing they can do on account of the pressure of the superficial fibres, and the fact that the width of the fibres shortens from two-thirds to one-third of the heart wall. This is in keeping with Borelli's idea of the formation of an "intumescence internally," and seems to fulfil all the requirements as regards timing.

(*b*) *The right ventricle.* Owing to the attachment of the two apices, the fulcrum of the left ventricle, the apex, may be taken as that of the right. Some writers (Luciani, 1911) even state that the right apex has a kind of traction on the left apex which has some effect in the causation of the cardiac impulse.

The fulcrum having been determined, we can proceed with the description of the contraction. As may be suspected from the anatomy of the fibres and the crescentic shape of the ventricle, the contraction may be described as the coming together of the right external wall and the septal wall. But there are a few points of interest to be added.

In most of the hearts put into the systolic state by boiling, an anterior concavity presented on the outer wall of the right ventricle. This could not

be due to any extraneous causes such as position of the heart while being boiled, and can only be due to the arrangement of the fibres. The concavity can probably be put down to the contraction of the trabeculae, which are numerous in the posterior and lower part of the cavity. The trabecular fibres aid the action of the weak external wall in pressing on the contents. It also makes the channel which appears in the upper part of the cavity on contraction more prominent.

In systole, the base of the ventricles is made wider in comparison with the auriculo-ventricular orifices (fig. 1). This is especially marked on the right side of the right auriculo-ventricular orifice, and, in the interior, a definite channel is found, running from the posterior part in the region of the right margin to the conus and then pulmonary artery. This is accentuated by the sinking in of the posterior part of the tricuspid valve, so that the most basal part of the ventricular wall, in systole, forms the inner wall of the channel. This has suggested to me a similarity with the valve which Pettigrew (1864, p. 470) describes in the same situation in the bird heart. This is muscular, and takes the place of an ordinary valve in the bird; and, in the human heart, the appearance in systole certainly suggests a protective influence on the right auriculo-ventricular ring, and also a directing influence on the course of the blood into the conus arteriosus. This contracts a little later, and then, after that, the semilunar valves receive some slight protection from the circular fibres round the junction of the conus arteriosus and the pulmonary artery (fig. 10).

### 3. The Joint Action of Auricles and Ventricles

In conclusion, the auricles and ventricles are considered together, and this we owe to Keith (1907). He pointed out the antagonistic action of the longitudinal fibres of the auricles and the ventricles.

The auricle contracts in the manner we have described, and during this the ventricle relaxes by its longitudinal fibres especially, and is drawn on to its load of blood by the pulling up of the base of the ventricles. Then in turn the ventricles contract, as has been described, sending the blood through its relatively fixed aortic base, and acting from the fixed apex to pull the auricular base downwards by means of the inner longitudinal fibres. This descent of the auricular base increases the dilatation of the relaxing auricle, and therefore the contents to be later expressed into the ventricle (Keith, 1907). This may be said to subscribe partly to the theory of "active diastole," but not, it must be noted, of the contracting chamber. It is "active" due to the contraction of the antagonistic muscles.

The movement of the auricular base downwards while the aortic base is fixed thus causes some tilting of the base obliquely from behind forwards, and is said to be a factor in the causation of the apex beat.

## SUMMARY AND CONCLUSIONS

1. The work upon which this paper is based has consisted in the dissection of the muscle fibres of the auricles and ventricles in both adult and foetal human hearts; in addition to the recording of the anatomical facts ascertained from the actual dissections, an attempt has been made to correlate the anatomical findings with the physiological point of view.

2. The specimens used for study have consisted of hearts removed from dissecting-room cadavers and hearts obtained from post-mortems. The former had all been preserved in 3 per cent. carbolic acid for from four to seven years; prior to dissection these were either washed in water or brought to the boil. The hearts from post-mortems were treated according to three different methods. The relative merits of the various methods are discussed; though there are advantages in having specimens prepared in several different ways, the best single method for general purposes has been found to consist in soaking the heart in 3 per cent. carbolic acid for at least six months, with subsequent washing in running water for 24 hours.

3. From the point of view of their anatomy, the fibres of the ventricles can be divided into three layers, superficial, middle, and deep. The anatomical terms used by Mall (1911) are continued here, as being the most suitable to be found in the literature. The superficial and middle layers are described for both ventricles together, while the deep layer is considered separately in each ventricle.

4. A brief outline of the more common variations met with in the ventricular musculature is given; these being classified according to the layers in which they fall. As regards the deep fibres, however, the ordinary anatomical results are so much only the average of the findings, that variations can hardly be given with any degree of certainty.

5. A synopsis is attached indicating the bare anatomical points regarding each bundle of ventricular muscle fibres.

6. A discussion of spontaneous rupture of the heart contains a *résumé* of the literature, and a report on the pathological appearances, macroscopical and microscopical, of four specimens of heart rupture. There were, however, no clinical details available. Thus, the only points that allowed of investigation were the site of rupture, and the etiology as judged from the state of the heart wall. In three of the four cases, the site of the rupture was the anterior wall of the left ventricle; and the etiological factor was in all four cases atherosclerotic change in the walls of the coronary arteries, this leading either to acute infarction, or to more chronic infarction with aneurism and the occurrence of rupture subsequently.

7. The fibres of the auricles are investigated from an anatomical point of view, and in this, assistance is obtained from splitting into the auricular septum from the posterior aspect. This is taken to indicate the original separation of the auricular septum into septum primum and septum secundum. The

fibres are described in two layers, and are not divided into actual muscles, as has been done by Papez (1920), but the course of the various fibres is given.

8. The anatomical points are applied to the action of the heart. Reference is made to Keith's work on the fulcra of the heart, and are noted in the subsequent discussion. The auricles are first studied apart from the ventricles, and from Lewis' findings on the times of contraction of various parts of the auricle, and the course of the fibres, an anatomical explanation is given of the contraction beginning around the mouths of the great veins. The two ventricles are next studied in turn. In the case of the left ventricle, the action of the deep bulbo-spiral muscle has been given a new significance, in its protective influence on the orifices at the base of the ventricle; and the method of fixation of the apex is explained by the arrangement of the fibres. In the right ventricle, the deep sino-spiral muscle has a somewhat similar action, and from its appearance in the contracted heart, shows a similarity to the muscular valve described in the heart of the bird. This type of valve can be credited with a directing influence on the course of the blood into the conus and pulmonary artery, and is continuous anteriorly with the supraventricular crest. Finally, the action of the auricles and ventricles is studied together, and the antagonistic action of the longitudinal fibres is stressed, a fact which again we owe to Keith.

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# TAURODONT TEETH IN SOUTH AFRICAN RACES

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## Introduction

In 1923 a number of remains, among them skulls and teeth, were discovered in two large rock-shelters at Zitzikama, Eastern Province, by Mr FitzSimons, Director of the Port Elizabeth Museum.

In the same year Prof. Raymond A. Dart pointed out the similarity existing between one type of skull discovered in the lowest levels of these rock-shelters and the Boskop remains.

In 1924 Dr Gordon D. Laing reported on the skulls (Strandlooper) from the higher and later levels of the same deposits at Zitzikama. Dr Laing concluded that the Strandlooper skulls showed a hybridisation of the Boskop race with the Bushman.

The teeth with which we are concerned are odd ones retrieved during the digging of these caves. They were received here unaccompanied by records of the skulls to which they belonged, but it is considered that the majority of them belonged to skulls of the superficial deposit, similar to those described by Dr Laing (i.e. Strandlooper skulls), and that two maxillary and two mandibular molars belonged to skulls from the lowest levels, similar to those described by Prof. Dart (i.e. Boskop skulls).

They were handed over to me by Prof. Dart for investigation and, for the reasons referred to above, they are described here as Strandlooper and Boskop teeth respectively.

*Strandlooper teeth.* A superficial examination of these odd teeth immediately revealed the fact that the molars (fig. 1, 1–4 and Plate I, *row A*) were markedly different outwardly from typical molar teeth of modern races, on account of the shortness of their roots and the relatively great length of their undivided portions, which must have been infra-alveolar when the teeth were present in their sockets (fig. 2, *A*).

The character of the chambers of some of these teeth, as revealed by sectioning on a revolving circular saw, afforded support to the view that these teeth differed greatly from typical modern teeth, for their pulp chambers were found to be relatively larger and to extend more deeply into that region of the tooth which in typical modern teeth is occupied by the roots (fig. 1, 1).

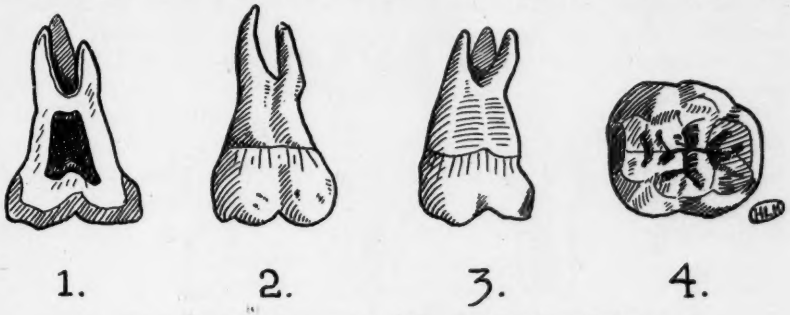



Fig. 1. Four typical examples of the molar teeth from Zitzikama.

*Boskop teeth.* These teeth were of the same general type as the Strandlooper teeth but were built on a larger and more generous plan (Plate I, *row B*). The roots of the lower molars are absent but the roots of the upper molars are present and exhibit a strong tendency to be fused into one solid mass. The relative size of the crown, root and undivided portion of these teeth is somewhat similar to the relative size of these parts in the Strandlooper molars.

Molar teeth with the characters found in these Zitzikama teeth, i.e. molar teeth with long infra-alveolar undivided portions, short or fused roots and relatively extensive pulp chambers, I had not seen formerly in any modern race (if infrequent third molar teeth are excepted). It is well known however that molar teeth with somewhat similar characters have frequently been discovered in fossil races (e.g. Neanderthal and Heidelberg).

In 1913 Sir Arthur Keith, writing on "Problems relating to the teeth of the earlier forms of prehistoric man," proposed that for "a curious process or condition of the molar teeth," i.e. "a tendency for the body of the tooth to enlarge at the expense of the roots," "we ought to have a distinctive name."

Provisionally, "for this condition or tendency" he proposed the name of "taurodontism," because, according to him, "the tendency for the body of the tooth to enlarge at the expense of the roots is a tendency to assume the

condition seen in the teeth of the ungulate or cud-chewing animals, e.g. the condition seen in the ox."

For "the opposite condition—that seen in the teeth of the carnivora—where the body of the tooth is above the alveolar margin," he proposed the name of "cynodontism."

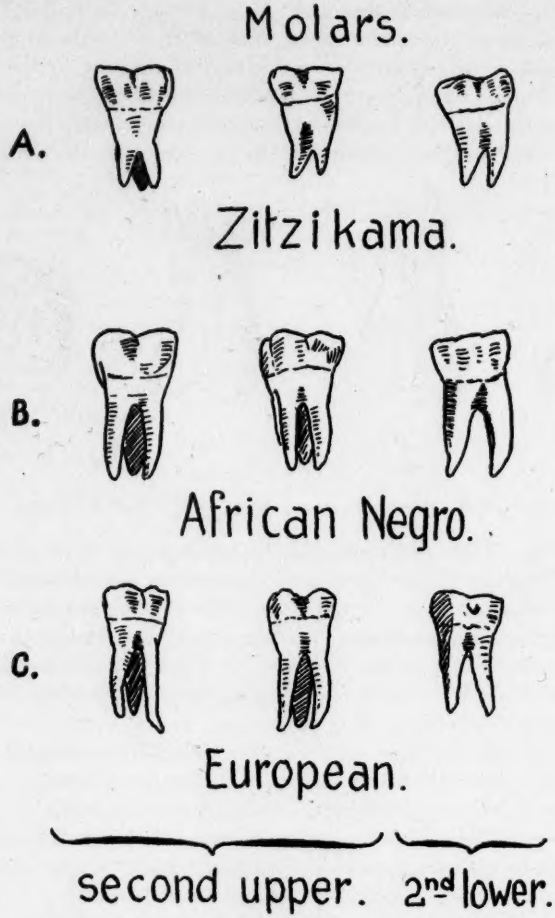



Fig. 2. Drawings of molar teeth of the Zitzikama peoples, African negro and European (natural size).

At a later date (1916) Sir Arthur Keith states that for "molar teeth" that "are large in crown and body and exceedingly short in root," he has "proposed the name of 'taurodont,'" and "to the more primitive form, seen in apes and also in modern types of men, the name 'cynodont' is given."

Accepting the terminology of Keith (1913) for this *tendency* in teeth, it is clear that the molar teeth discovered at Zitzikama exhibit "taurodontism."

Taurodontism, according to recent writers, is exceedingly rare in modern races, but occasionally, as pointed out by Keith himself, by Mummery (1923) and by other writers, third and other molar teeth are met with that show the condition. Kramberger (1907) has stated that the Eskimo sometimes exhibits a slight degree of taurodontism and Adloff (1910) has figured a taurodont tooth in a European.

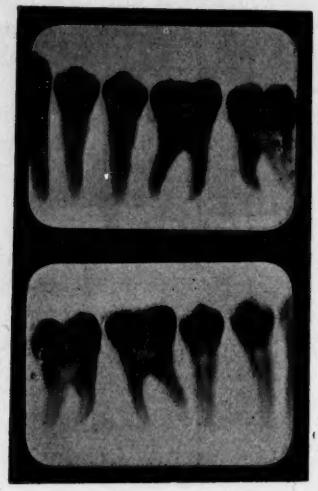
Taurodontism has been shown, as stated above, to be a character of certain fossil races (Heidelberg and Neanderthal).

The peculiar characters of the teeth in the Neanderthal race were described at length for the first time by Dr Paul Adloff (1908), who showed that the teeth of Neanderthal man, especially those discovered (1907) by Dr Gorganovic-Kramberger at Krapina, were long and infra-alveolar in their undivided portions, large in their crown, short or fused in their roots and possessed of very enlarged pulp chambers.

The name "taurodontism" was subsequently (1913) proposed by Sir Arthur Keith as the result of the necessity for introducing a term which would succinctly express this combination of characters. According to Keith (1916) taurodontism "is present to a greater or lesser degree in the teeth of all members of the Neanderthal race. It is a character of that race."

Many authorities, whose opinions will be stated more fully at a later stage, regard the "degree of taurodontism in the Neanderthal teeth" as a character of specific rank, i.e. a character which assists in demarcating Neanderthal man from modern (sapient) man. Unfortunately, these authorities have not stated, so far as I am aware, what "degree" of taurodontism they consider a character of specific rank, although the necessity for such a statement is evident since Keith has shown that the "degree of taurodontism varied widely in the examples of Neanderthal man so far discovered" (according to that writer the degree "was extreme" in a number of the teeth in the Krapina Neanderthaloids and "less marked" in the teeth found at Spy. Tomes (1923) states that "only 50 per cent. of the Krapina teeth presented peculiarities of the roots in any marked degree" and that the Spy molars could pass for molars of the modern type).

I have found it essential for the purposes of this communication to introduce more precise terms that will indicate the different "degrees" of taurodontism observed in the teeth examined by me. Accordingly it is proposed that the extent of vertical deepening of the undivided portion at the expense of the root seen in the teeth of the Heidelberg jaw ("a considerable degree," according to Keith (1916)) be taken as a mean; the extent of the development being known as "meso-taurodontism" and the teeth as "meso-taurodont teeth" (fig. 3, *C*). The extent of the development seen in the teeth of some of the Krapina Neanderthaloids (fig. 3, *D*) may then be denoted by the term "hyper-taurodontism," the teeth being called "hyper-taurodont



Skiagram 1. Skiagrams of the lower premolar and molar teeth of a Bantu-Boskop hybrid. (The third molar teeth are erupted but not shown in the skiagrams.)

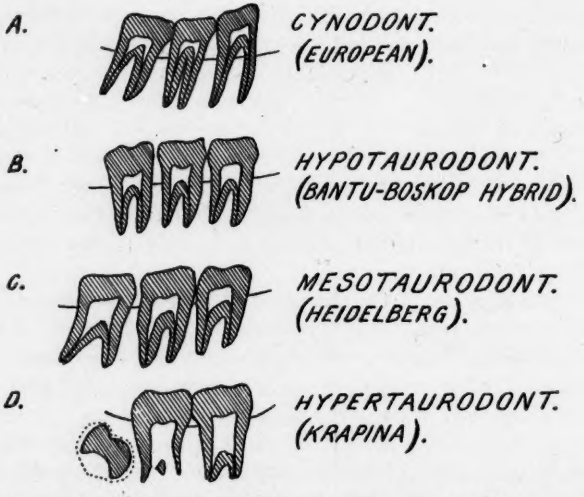



Fig. 3. Drawings from skiagrams of the lower right molars of modern European (*A*), Bantu-Boskop hybrid (*B*), Heidelberg mandible (*C*), Krapina mandible (*D*), to illustrate different degrees of taurodontism. ((*C*) and (*D*) after Professor Keith.)

teeth"; while the degree of development seen in the teeth of some South African Bantu-Boskop hybrids (fig. 3, *B*) may be called "hypo-taurodontism" and the teeth "hypo-taurodont teeth." Prof. Keith's terms, i.e. taurodontism and taurodont, with their opposites, cynodontism and cynodont, are still by this nomenclature retained as general descriptive terms for the tendencies exhibited by human teeth.

Although there is no doubt that the morphological characters of the Zitzikama teeth are not identical with those of the Neanderthal teeth, the presence of taurodontism in the molars from Zitzikama, and in molars of other South African people subsequently examined, warrants a detailed description of these teeth in this report.

## Material

Unfortunately the skeletal material from Zitzikama had been returned to Port Elizabeth before taurodontism was discovered in the odd teeth. Hence a description of the teeth in the skulls is not possible at the present time.

The odd Zitzikama (Strandlooper) group consisted of seventy teeth. Fifty-seven of these are complete or partially complete teeth. Twelve are crowns (molar) of teeth. The remaining tooth has the characters of an ill-formed supernumerary premolar.

As stated formerly, the other odd Zitzikama (Boskop) group consisted of two maxillary and two mandibular molars, both appearing to belong to one individual.

Skulls utilised for examination of the teeth in other South African races were first of all those from a loan collection of Bush-Hottentot skeletons from the McGregor Museum of Kimberley[1]. Most of these skulls formed the basis of Dr R. Broom's communication (1925) to the Royal Anthropological Institute on the craniology of the yellow-skinned races of South Africa. They have been classified for the purposes of the paper by Mr H. S. Gear as follows:

1. Pure Bantu skulls ... ... ... ... ... 6 specimens
2. Pure Bush skulls ... ... ... ... ... 9 „
3. Bantu-Bush hybrid skulls ... ... ... 2 „
4. Bantu skulls showing Boskopoid element ... 5 „
5. Bush skulls showing Boskopoid element ... 3 „
6. Bush skulls showing Australoid (Broom) element 8 „

Total number of skulls in this collection: thirty-three.

In the second place, part of the extensive collection of skulls in the Anatomy Museum of this University was utilised. This collection has been classified as follows:

1. Bantu skulls ... ... ... ... ... 81 specimens
2. Bush skulls ... ... ... ... ... ... 6 „

[1] I am indebted to Miss M. Wilman, Director of the McGregor Museum, Kimberley, and also to the Trustees of that Institution, for lending this valuable collection of skulls.

3. Bantu-Bush hybrid skulls ... ... ... 5 specimens
4. Bantu skulls showing Boskopoid element ... 6 „
5. Bush skulls showing Australoid element ... 4 „

Total number of skulls in this collection: one hundred and two.

Finally, there were examined the dentitions in twelve skulls of known Bantu tribes. These twelve skulls are the property of the South African Institute for Medical Research and were lent to us by the Director, Sir Spencer Lister.

In all, therefore, the teeth in one hundred and forty-seven skulls were examined.

## Remarks upon: 1. Dental Terminology. 2. Internal and External Characters as Criterions for the Diagnosis of the Conditions exhibited by Human Teeth. 3. Classification of the Characters of the Molar Series, as a whole, in a single Individual

### 1. *Dental Terminology*

According to Tomes (8th edit. 1923):

for the purpose of description the three external parts of a tooth are distinguished by name, viz. the crown, neck and root. This distinction is made in describing human teeth, and is applicable to the great majority of mammalian teeth, though there are some forms in which no such differentiation of parts can be seen. The crown is that portion which is exposed above the borders of the gum, and is in human teeth coated by enamel; the neck is that portion which corresponds to the edge of the gum, and intervenes between the edges of the bony sockets and the edge of enamel; the root is that part which is enclosed within the bony socket, and is covered by cementum.

Of these it is to be remarked that the "neck," although a convenient and necessary term for descriptive purposes, marks an arbitrary division of less importance than that expressed by crown and root; also that, although this division into three parts can be made in the case of socketed teeth of limited growth, no such distinction of parts can be made in teeth of perpetual growth.

According to the writings of Hopewell-Smith (1913), Mummery (1923) and others, Tomes' description of teeth, as quoted above, is correct. These writers recognise three parts of a tooth and define these parts in a manner similar to that adopted by Tomes.

In actual point of fact, however, where measurements of teeth are made, that portion of the tooth which intervenes between the crown and the root, i.e. the portion that Tomes and others call the "neck," is disregarded and the tooth is looked upon as consisting of crown and root only (*vide* Hopewell-Smith's *Dental Anatomy and Physiology*, p. 174 and following pages). This procedure, although loose, would be satisfactory enough if one had to deal only with cynodont teeth, where the intervening portion is small (approximately 2·5 mm.) in size and sufficiently short to be regarded as "arbitrary."

In taurodont molar teeth, on the other hand, Tomes' definitions, as quoted

above, cannot be applied because not only the roots but also a considerable part of the undivided portion of the tooth above the roots, although perhaps "not covered by cementum," nevertheless "is enclosed within the bony sockets" (*vide* fig. 3).

Further, with the great lengthening of the interval between the crown and the root the intervening part of the tooth can be no longer regarded as "arbitrary," but is on the contrary a striking and independent part of its anatomy and is, equally with the crown and the root, deserving of a specific descriptive term.

In applying a term to this middle portion of the taurodont molar tooth it is obvious that the term "neck," as defined by Tomes, is unsatisfactory, because in this type of tooth the middle part no longer "corresponds to the edge of the gum" and no longer "intervenes between the edges of the bony sockets and the edge of enamel." The term "body" has been used by Keith

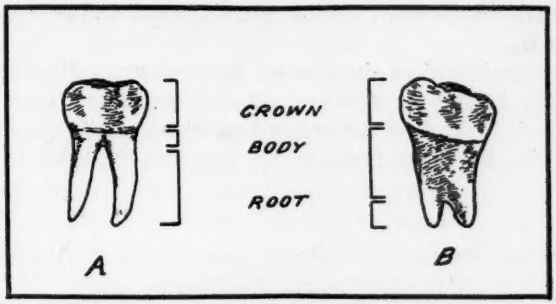



Fig. 4. Diagram to illustrate the parts of a cynodont tooth (*A*) and taurodont tooth (*B*), showing the measurements taken.

(1913) to describe this region and has found a certain currency in the literature, although he has in no place, to my knowledge, pointed out the necessity that exists here for the introduction of a new term, nor expressed clearly what the significance of the term "body," as used by him, actually is.

In this investigation it was essential to divide the taurodont molar tooth into three regions and to measure these regions separately (fig. 4). I have adopted as more suitable the term introduced without definition by Keith, to distinguish the middle portion of the tooth, namely, the *body*. I have further taken the liberty to define the *body* for the purposes of this report as that portion of the tooth which intervenes between the lower edge of the enamel and the upper end of the groove which usually marks the division or partial division of the roots and which seems to correspond with the uppermost extent of the cementum. Tomes' definition of the *crown*, i.e. that portion of the tooth which is exposed above the borders of the gum and is in human teeth covered by enamel, can be and is retained. The *root*, however, is defined

by me as the divided or partially divided portion of the tooth that is covered by cementum, is enclosed within the body socket and intervenes between the lower border of the body, as defined above, and the base of the bony socket.

The term *body*, so defined, may be applied to cynodont teeth, but even in these it does not necessarily correspond with the "neck" as defined by Tomes, and in view of the fact that the term "neck" as hitherto used by investigators *is* "arbitrary" and is usually entirely neglected in measurements taken, it is suggested that it should not in future be used for the purpose of anthropometric discussion (*vide* fig. 4).

It must however be remembered that the term "neck," as used by Tomes, while perhaps of no value anthropometrically, is of distinct value descriptively in another sense, namely, that while there is usually a very marked constriction at the junction of the enamel and cement in cynodont deciduous teeth, such a constriction is less marked in cynodont permanent teeth. Wherever the term (neck) is used in this paper it has reference to this character of constriction at the enamel-cement junction. Such a neck is also usually *absent* from taurodont teeth.

Following the definitions given above, the mean proportions of the crown, body and root lengths of cynodont (Bantu) maxillary molars (maxillary molars predominate in the Zitzikama collection) are 7, 2, 11 mm. of the whole respectively, i.e. the crown and root are long and the body is exceedingly short (fig. 4).

### 2. *Internal and External Characters as Criterions for the Diagnosis of the Conditions exhibited by Human Teeth*

Although it was primarily for external characters of teeth that the term taurodontism was proposed (*vide* statement of Keith given above), the size of the pulp cavity (i.e. internal characters), as revealed by radiographic examination, has been customarily taken as the basic criterion upon which the diagnosis of taurodontism has rested.

For this reason it is necessary to enquire whether internal or external characters afford the better criterion for the diagnosis of the conditions exhibited by human teeth.

Concerning internal characters it must be pointed out that, since the pulp is not a fixed organ, the "size and form of the pulp cavity are subject to manifold individual variations" (Loos, quoted by Hopewell-Smith, 1919).

It is relatively large in early life but decreases in size later in life, due to factors which are not as yet adequately known.

According to Campbell (1925) the decrease in size is due to *attrition*. The dentine being exposed, its fibrils are irritated and the odontoblasts stimulated to active formation of secondary dentine, which reduces the cavity size.

The investigations of Courtney Lyne (1916) on the formation of dentine, based on a very wide series of teeth at different ages, showed, according to

him, that the pulp cavity is reduced by *age*. That writer says that the pulp cavity, taking the average of one age with another, is steadily decreasing in size during life and that, *à priori*, a large pulp cavity indicates a tooth from a young animal and a small pulp cavity indicates a tooth from an older animal. It is also well known that a gradual change of the tooth-pulp into calcified tissue, as a result of *disease*, e.g. caries, and *injury*, proceeds to obliterate the pulp cavity and reduce its size.

Taurodont teeth are open to the same influences which reduce the pulp cavity in cynodont teeth. While, therefore, the presence of an enlarged pulp cavity may be conclusive proof of taurodontism, the absence of an enlarged pulp cavity is not necessarily proof that a tooth exhibits cynodontism. This fact is well known by some writers and Prof. Boule (quoted by Sollas, 1924) has in fact shown that the pulp cavities in some of the Neanderthal molars are exceedingly small; *even although the external characters of these teeth are of the taurodont type.* Hence, in the writer's estimation, internal characters, as revealed by radiographs, may be deceptive and may render nugatory conclusions based on these criterions alone. That is to say, internal characters, although admittedly of paramount importance as secondary or indirect evidence of the morphological characters of a tooth, are not in themselves conclusive evidence of the condition exhibited.

On the other hand, although no two dental organs possess exactly similar morphological characteristics, the external parts (crown, body and root) of any individual tooth, once formed, remain fairly constant in form throughout the life history of the tooth. The crown can, it is true, be worn away by attrition or disintegrated by caries; the body, as defined above, may be slightly altered by disease and the roots can be reduced slightly in size by absorption or enlarged slightly by deposition of cement. But, in its chief anatomical features, i.e. the relative proportions of crown, body and root, a tooth remains fairly fixed in external form during its existence. Moreover, in alteration of external form, it may be stated that the body, upon whose size the diagnosis of the condition of the tooth especially depends, is customarily the least affected of any by the above-mentioned factors.

As has been stated above, external characters afford adequate evidence for the diagnosis of the condition exhibited by some of the Neanderthal molars. Likewise, in this investigation it has been found that external characters and dimensions afford more reliable evidence of a tooth's morphological characters, whatever its age or however much it may be worn away, than internal characters. For example, it was found that the relative size of the parts—crown, body and root—of, among others, a second molar examined was 7 : 4 : 6 mm. respectively. The body of this tooth was long and infra-alveolar, the roots were short and fused, and yet the pulp cavity of this tooth was exceedingly small. That is to say, the external characters and dimensions betrayed the fact that this tooth was taurodont even although the internal characters afforded no indication whatever of this fact.

For these reasons the external characters of the teeth examined by me, as revealed by careful measurements and macroscopic examination, have afforded the basic criterion for the diagnosis of the conditions exhibited by these teeth.

### 3. *Classification of the Characters of the Molar Series, as a whole, in a single individual*

Although, as stated formerly, the external characters of an *individual* molar tooth remain fairly constant throughout the life history of that tooth, it is to be noted that in any *series* of molar teeth in a single individual the external characters (and internal characters) vary gradually from before backwards, i.e. in passing from the first to the third molar. In other words, if the second molar tooth is a typical meso-taurodont tooth the first molar is not so pronouncedly meso-taurodont, while the third molar is generally more markedly meso-taurodont and may tend towards a condition of hyper-taurodontism.

This general transition as we proceed from the front to the back of a molar series, and which I have never seen recorded, nor have ever witnessed personally, as progressing in the reverse direction, is due, as previously discussed, to factors of age, attrition and perhaps still further undiscovered causes.

Whatever the cause, it may be stated categorically that the first molar in any molar series tends less than any of the other molars to the condition of taurodontism and that the second and third molars tend more to the condition of taurodontism.

This fact is generally recognised and, as pointed out by Tomes (1923), some of the Krapina (taurodont) molar series afford excellent evidence of this transition in passing from the front to the back of a molar series (*vide* fig. 3, *D*). The same phenomena can be seen in radiographic pictures of the molar series in the Heidelberg jaw.

Although, however, the characters of the teeth in a molar series vary appreciably in this manner, it has been my uniform experience during this investigation to find that the condition exhibited by the molar series, as a whole, fluctuates around that exhibited by the second molar.

Thus, in all the dentitions examined, if the second molar was meso-taurodont the first and third molars were also meso-taurodont, even although the characters of the former tooth were inclined towards hypo-taurodontism and those of the latter towards hyper-taurodontism. Likewise, where the second molar was hypo-taurodont the first and third molars were hypo-taurodont, although definitely exhibiting the character to a lesser and greater degree respectively than the second molar.

Owing to the fact that the condition of the molar series as a whole fluctuates around that exhibited by the second molar, it is convenient, for the purposes of classification of any molar series *as a whole*, to accept the second molar tooth as the standard tooth upon which to base the diagnosis of the

condition of the series. Accordingly, in this report, the second molar has been accepted as the standard tooth of the series and the terms hyper-taurodontism, meso-taurodontism, hypo-taurodontism and cynodontism have special reference to the type of the second molar in the dentitions examined.

Stated briefly, the conclusions arrived at are the following:

1. A tooth consists of three parts, namely, a crown, a body and a root.

2. A cynodont tooth has a relatively long crown and root and a relatively short body.

3. A taurodont tooth is relatively long in crown and body and relatively short in the root.

4. Internal characters of a tooth, although of considerable service as secondary or indirect evidence of the morphological character of the tooth, are not in themselves conclusive evidence of the condition of the tooth.

5. The external characters of a tooth and the relative proportions of its crown, body and root, as revealed by macroscopic examination and careful measurements, afford the best criterion for the diagnosis of taurodontism or cynodontism.

6. The characters of the molar teeth in a molar series in a single individual fluctuate around those exhibited by the second molar tooth. The second molar tooth in a molar series may therefore be taken as the standard tooth of that series for the purpose of classification of the characters of the series as a whole.

### Zitzikama Strandlooper Anterior Teeth

The majority of these teeth conform to the Bantu type but a few differ slightly from that type.

Thus, one second maxillary incisor and two maxillary canines exhibit well-marked marginal ridges on their lingual surfaces, which produce a roughly triangular shallow concave central fossa on this aspect of the teeth. Teeth with the same characters, according to Hrdlička (1920), "occur frequently in yellow-brown peoples, such as Malays, Mongolians, Chinese and Japanese but are less common to rare in other racial groups." Because they "resemble more or less an ordinary coal shovel" they are termed by Hrdlička "shovel-shaped teeth." That writer recognised three grades of "shovel shapes" in the teeth examined by him and adopted the term "shovel" for all the better developed grades; "semi-shovel" for the less well-developed grades and "trace-shovel" for slight but distinct indication of the character.

Accepting this terminology, the Strandlooper maxillary canines are "semi-shovel"; the incisors are "trace-shovel."

Four first maxillary incisors are also of interest because the lines which represent their proximal surfaces converge rapidly towards the necks. In other words, these teeth exhibit marked excess in their transverse diameters at their biting edges.

Azoulay and Regnault (1893) have stated that this character is not infrequently found "in inferior races" and rarely found in "the yellows, the

European and Hindus." Leon Williams (1914), on the contrary, although expecting to find racial differences in the form of the incisors, found that no such differences existed and that "three primary forms of teeth are common to all races."

Examination of the teeth in South African Bantu races afforded support to Leon Williams' view, for it was found that in these races three forms of upper first incisor teeth may be recognised. It must be pointed out, however, that it has been my experience to find that the form of incisor tooth described above (Class II, of Williams) is the rarest form in typical South African Bantu races. That is to say, the type of incisor tooth discovered at Zitzikama is not identical with the typical type of incisor tooth found in living Bantu races.

### Zitzikama Strandlooper Molars

Fourteen complete molars (three of which are lower molars) and twelve molar crowns (four of which are the crowns of lower molar teeth) were found in the Zitzikama Strandlooper collection.

*The Complete Teeth.* One of the complete lower molars and four of the complete upper molars are, unfortunately, third molar teeth and it was decided that these should not be described in detail (on account of the variability in size and shape of such teeth in all races). It is to be noted, however, that these third molars belong to the same general type and exhibit the same characters in the same or even a more marked degree than those now to be described

1. *External Characters.* The complete molars (seven from the upper and two from the lower jaw) are, with three exceptions (two upper and one lower tooth), exceedingly small in all respects. The average mesio-distal length of the crown of the five small maxillary molars is only 9·6 mm., the average bucco-lingual width is 10·5 mm. (*vide* fig. 5) and the average (extreme) length, from the apex of the lingual root to the most prominent part of the mesio-lingual cusp (which is slightly worn in all cases), is approximately 17·0 mm.

The dimensions of the remaining two maxillary molars do not differ greatly from those of modern Bantu races.

The five maxillary molars referred to above are remarkable, however, not only in their actual smallness, as compared with typical (Bantu) human teeth, but also in the shortness of their roots relative to the length of their crowns and in the large size of their bodies; in other words, in the relative growth of their bodies at the expense of their roots (fig. 2). Thus, the average length of the lingual root of the five teeth is only 7·0 mm., the average length of the crown (slightly worn) 6·0 mm., and the average length of the body 5·1 mm.

The relative proportions of crown, body and root of the remaining two maxillary molars are approximately similar to those of these five teeth.

The proportions of the crown, body and root of the Strandlooper maxillary molars are therefore approximately 6 : 5 : 7 mm., the extremes being

6 : 6 : 7 mm. and 6 : 4 : 7·5 mm. That is to say these teeth, compared with cynodont (Bantu) teeth, have slightly smaller crowns; bodies that are relatively and actually larger, and roots that are relatively and actually shorter, than those of cynodont Bantu teeth.

The constriction or "neck" at the junction of the enamel and cement varies from being ill defined to being entirely absent.

The external characters, dimensions and relative proportions of the crown, body and root of one of the lower molars in this collection are similar to those of the upper five maxillary molars, while the other lower molar is a much larger tooth and exhibits the character of fusion to a marked degree. The relative proportions of its crown, body and root are approximately 7 : 8 : 5 mm. respectively.

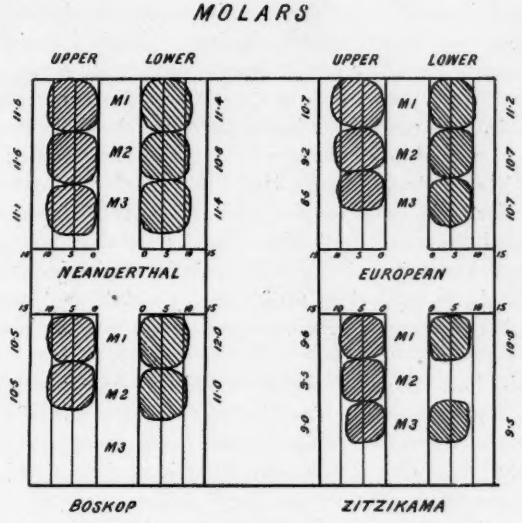



Fig. 5. Diagram showing the development of molars in Neanderthal, European, Boskop and Zitzikama man; the teeth are placed in the diagram so as to contrast their lengths or mesio-distal diameters. The parallel lines which cross the length of the crowns are 5 mm. apart. (Neanderthal and European man after Campbell.)

Consequently, as far as the outer aspect is concerned, taurodontism is exhibited by these Strandlooper molars. I consider that these teeth are entitled to be placed in the meso-taurodont class, as defined above.

2. *Internal Characters.* In two instances the internal characters of the Strandlooper molars were revealed by sectioning and the internal characters of the remaining teeth were revealed by radiographic examination.

Although, as stated formerly, the pulp cavities in the majority of these teeth are relatively large, actually they are not larger than the pulp cavities of adult cynodont (Bantu) teeth, except in two instances.

One, an upper first molar with its root apices not yet completely closed, has a pulp cavity which measures 5·0 mm. in the bucco-lingual direction, slightly less in the mesio-distal direction, and 6·0 mm. in the vertical direction.

Another upper molar, a second probably, has a pulp cavity that measures approximately 4·5 mm. in all directions. This tooth is well worn and possibly belonged to an individual of much more than adult years. The remaining teeth have pulp cavities that vary in size. In two instances the cavity is considerably reduced in size by deposit of secondary dentine. In the other teeth the cavity in no instance exceeds 3·5 mm. in diameter, but in these teeth also there is evidence of deposit of secondary dentine.

From this it is concluded that in the teeth of younger individuals of the Strandlooper race the pulp cavities must have been considerably larger than in the worn and, in many cases, aged specimens described here.

*The Crowns.* The molar crowns require no detailed description. Their occlusal surfaces do not differ greatly from those seen in recent negroid races except that four lower molar crowns exhibit crenation or wrinkling of their enamel (fig. 1, 4). This condition I had not seen previously in any *adult human* teeth nor do I know of any instances recorded in European or Bantu races. Gregory (1921) has stated, however, that "lower molar crowns with wrinkled surfaces" are found in Bush peoples, and Boule (1923) has stated that the (taurodont) Taubach molar tooth (described by Nehring, 1895) exhibited the same condition. I regret that the Bush material available for study in this Department lends no support to Prof. Gregory's statement and it therefore appears probable that *even in Bush peoples crenation of the enamel is an exceedingly rare condition.*

Many of the lower molar "crowns" in this group possess five cusps and are larger than the crown of the small complete lower molar referred to above. Likewise, a few of the upper molar "crowns" are as large as the crowns in Bantu races, but the majority do not differ in their dimensions from the crowns of the small Strandlooper maxillary molars.

Since the roots and bodies are absent, there is nothing to indicate that these "crowns," as well as the "complete teeth," are not crowns of meso-taurodont teeth. The resemblance in form and size of some of them to the crowns of the complete teeth and the fact that they were discovered in the same deposits at Zitzikama as those, appear to warrant their inclusion in the same meso-taurodont group.

We may conclude therefore that meso-taurodont teeth occurred with considerable frequency in the Strandloopers, which are known to be Bush-Boskop hybrids (Laing, 1924).

### Zitzikama Boskop Molars

It was evident on inspection that, although these teeth possessed the same general characteristics as the Strandlooper teeth, they were markedly larger in all their dimensions and slightly different in some of their anatomical

features (Plate I, *row B*) (fig. 6). The two maxillary molars (one, a first molar, the other, a second molar) are most remarkable. They exhibit complete fusion of their mesio-buccal and lingual roots, thickening and enlargement (not elongation) of their disto-buccal roots and overgrowth of their bodies.

It must be noted, however, that the fusion of their roots is not due to an approximation of the roots—the result of retrograde development—but is due rather to an opposite process, namely, an extension of the body of the tooth into that region which in cynodont teeth is occupied by the roots. That is to say, the roots of these teeth were never distinct to become fused later; the joined condition is one of initial development, brought about by a downward extension of the tooth body at the very earliest stage of its development.

The dimensions of their crowns are greater than those of the crowns of many Bantu molar teeth (*vide* fig. 5). The relative proportions of crown, body and root it was found impossible to ascertain with any degree of accuracy, owing to absence of fragments of the teeth at the junctions of these parts.

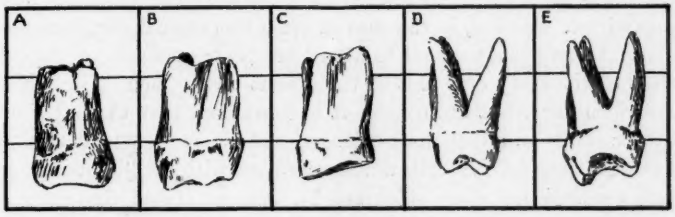



Fig. 6. Mesial aspect of upper molars of Neanderthal man (*A*); Zitzikama man (*B*); Boskop man (*C*); European man (*D*); and Chimpanzee (*E*). (Natural size.)

There is, however, no doubt that the crowns and bodies are relatively larger and that the roots are relatively and actually shorter than those of cynodont teeth (*vide* fig. 4).

Although these two Boskop maxillary molars are not as markedly hyper-taurodont as some of the Krapina molars, I consider that their characters entitle their inclusion in the same hyper-taurodont class, and accordingly they may be termed hyper-taurodont teeth.

The two lower molars lack their roots, but it is evident from inspection that when these were present they were not fused but divergent.

These teeth are also of large size (fig. 5) and their crowns each possess five cusps and are longer in the mesio-distal than in the bucco-lingual directions. Their bodies and pulp cavities are slightly larger than those of typical Bantu teeth.

For these reasons it is considered that these teeth probably exhibited the condition of hypo-taurodontism. The conclusion is therefore warranted that hyper-taurodont and hypo-taurodont teeth occurred in South African Boskop races.

### Taurodont Molar Teeth in other South African Races

It was desired to ascertain: (1) whether taurodont teeth occur in living South African races, (2) whether the condition of taurodontism appears in as marked a degree in living South African races as in the teeth of the Zitzikama peoples described above.

The entire collection of skulls utilised for this investigation has been detailed earlier in this paper. Collectively, they fall naturally into four main groups:

1. Bantu group.
2. Bush group.
3. Korana group (Australoid of Broom).
4. Bastard group.

The dentitions of these skulls were not absolutely complete, for teeth had been lost, not only before death but also post-mortem. The cheek teeth, however, are present in one or both sides of the upper or lower jaw in all the skulls examined. Further, in the case of teeth lost after death, the condition of the socket was usually found to afford adequate evidence of the external characters of the body and root of the absent teeth. The age of the skulls and dentitions vary, but in all cases it is considered that the individuals to whom these skulls and dentitions belonged had attained at least adult years.

All observations on the teeth were carried out with the aid of radiographic (indirect) examination (*vide* skiagram 1), but, as stated formerly, macroscopic examination and careful measurements of the crown, body and root afforded the basic criterion for the diagnosis of taurodontism.

Table I. *Showing the occurrence of taurodontism in South African races*

| Race | Number of Skulls | Hyper-Taurodont Skulls | Meso-Taurodont Skulls | Hypo-Taurodont Skulls | Cynodont Skulls | Percentage of Taurodont Skulls | Percentage of Cynodont Skulls |
|---|---|---|---|---|---|---|---|
| Pure Bantu | 99 | 0 | 0 | 0 | 99 | 0·0 | 100·0 |
| Pure Bush | 15 | 0 | 0 | 0 | 15 | 0·0 | 100·0 |
| Bantu-Bush hybrids | 7 | 0 | 0 | 0 | 7 | 0·0 | 100·0 |
| Bantu with Boskopoid element | 11 | 0 | 3 | 1 | 7 | 36·3 | 63·6 |
| Bush with Boskopoid element | 3 | 0 | 1 | 0 | 2 | 33·3 | 66·6 |
| Bush with Australoid (Broom) element | 12 | 0 | 3 | 2 | 7 | 41·6 | 58·3 |
| Totals ... | 147 | 0 | 7 | 3 | 137 | 6·8 | 93·7 |

Diagnosed in the manner stated above, taurodontism was found to occur in the teeth of living South African races. Classified on the basis of the second molar tooth, the extent to which the condition was developed and the frequency of occurrence of the condition in the dentitions examined is shown figuratively in Table I.

It will be seen from that table that taurodontism appears in as marked a condition in living South African races as it did in Zitzikama peoples. Further, it will be seen that taurodontism is absent from the teeth of pure Bantu and Bush peoples and also from the teeth of Bantu-Bush hybrids. The pure Bush and the pure Bantu stocks must therefore be cynodont.

On the other hand, in bastards, where the elements of fusion are Bantu or Bush with Boskopoid or Australoid peoples, taurodontism occurs with some degree of regularity—roughly in 30 per cent. of the bastards examined.

Where the elements of fusion are Australoid and Bush the condition occurs slightly more frequently than where the elements of fusion are Boskop and Bush or Boskop and Bantu. There is, however, evidence from this incidence to demonstrate that taurodontism was a feature of both the Boskopoid and Australoid peoples of Southern Africa.

We may conclude that:

1. The Bantu and Bush peoples of Southern Africa possess teeth of the cynodont type.

2. Taurodont teeth are, however, found in living South African races.

3. The condition of taurodontism is developed to the same extent in living South African races as in the teeth of the Strandlooper and Boskopoid peoples from Zitzikama.

4. Taurodontism occurs in South African hybrids where the elements of fusion are Australoid or Boskopoid with cynodont types like the Bantu or Bush races. Taurodontism is therefore a character of South African Australoid and Boskopoid peoples.

5. Taurodontism occurs roughly in 30 per cent. of such hybrids and therefore appears to act as if it were a Mendelian recessive character in the proportion of its emergence in hybrid stocks.

6. Taurodontism appears to be a character which breeds true in the Mendelian sense and therefore must be a character of at least *variety* rank.

7. Since taurodont races can intermingle with cynodont races of mankind and produce fertile offspring, taurodontism is not a character of zoological *species* rank.

8. Races which equal one another in a character demonstrated to be of *variety* rank are probably more closely related to one another than those not exhibiting the character.

9. The South African Australoid and Boskopoid peoples are more nearly related to one another than either people is to the Bantu or Bush stock. Inversely, the Bantu and Bush races are more nearly related to one another than either race is to South African Australoid or Boskopoid peoples.

## The Significance of Taurodontism

As of late years many inferences have been based upon taurodontism in the teeth of fossil man, the occurrence of taurodont teeth in modern races warrants an inspection of the significance of any new facts emerging from such a study as the present one.

In Neanderthal man the occurrence of taurodont teeth has been used as an argument that recent man cannot have descended from that race of man but belongs to a separate stock which in early times supplanted Neanderthal man, who died out.

The opinion that the taurodont teeth of Neanderthal man do not represent a stage in the evolution of modern cynodont teeth was first advanced by Adloff (1908), who considered that the *degree* of taurodontism exhibited by the teeth of that race was a specialised or retrograde character, not a primitive feature. Keith (1913), after entertaining the contrary view (1908), has now become a convert to the idea that taurodontism in the Neanderthals is a specialised character. According to him, taurodontism takes the Neanderthal race away from the ancestral line of modern man.

Gregory (1921), however, considers that "at least a moderate degree of taurodontism is a primitive feature for the Hominidae" and that the taurodont teeth of Neanderthal man, or some of them, may be structurally ancestral to teeth of the modern cynodont type.

Although it has been stated that taurodontism is the opposite to what obtains in anthropoids and primates generally, it is a remarkable fact that data concerning the external characters and relative sizes of the crown, body and root of molar teeth in primates other than man are either inaccessible or non-existent. That is to say, there is no evidence to prove that taurodontism, diagnosed by external characters and dimensions as suggested here, is never a character of the dentitions in at least some branches of the anthropoids.

Further, even if it be demonstrated that taurodontism does not occur in modern anthropoids, if Prof. Gregory (1920) and Prof. Miller (1915) are correct in assigning the Taubach molar to a fossil Pleistocene chimpanzee, there is evidence that taurodontism is known in the teeth of some *fossil* members of the anthropoid group. The Taubach molar has been figured by Keith as an example of a taurodont tooth with the "Neanderthal characters," and there appears to be considered evidence in favour of the view that this tooth belongs to no known member of the human family.

It has never been shown conclusively that the condition of taurodontism is not a primitive feature for anthropoids and, even if it had been so shown, since the anthropoids are themselves probably specialisations from the primate stem, the absence of taurodontism from the teeth of the living representatives of this group does not warrant the conclusion that taurodontism is a specialised character for the Hominidae.

When we come to examine the teeth of primitive man we find that the

teeth of Pithecanthropus (possibly the oldest human fossil known), although perhaps definitely of the cynodont type, are known to be highly specialised and therefore not available for comparison here.

The teeth of Eoanthropus, according to Gregory (1921), possess "a pulp cavity that is deeper than is common among modern teeth" associated with primitive features of the jaw and dentition. The relative proportions of crown, body and root have not, so far as I am aware, been published, but, from the condition of the pulp cavity, it appears not improbable that some degree of taurodontism is exhibited by the molars of the fossil.

In Heidelberg man who, it has been suggested, is a pre-Neanderthal, the teeth are likewise of the taurodont (presumably meso-taurodont) type, even although the crown patterns of the teeth and many of the characters of the jaw are of admittedly primitive human type.

In the Neanderthals taurodont teeth are also of frequent occurrence. In that race also, taurodontism is found associated with primitive features of the dentition, and although some writers claim that all the teeth exhibited taurodontism, the available records show that this was not the case. According to Tomes (1923) only 50 per cent. of the Krapina teeth were markedly affected by the condition and the molars of the Spy skulls could pass for molars of the modern cynodont type. Kramberger's work (1907) shows Neanderthal teeth with quite distinct and lengthy roots and bodies of the cynodont type. That is to say, the teeth of the Neanderthals varied from teeth of the massive taurodont type to teeth that cannot be distinguished from cynodont teeth.

This variation would find a natural explanation from the facts brought forward here if we regard the Neanderthals as a bastard race—taurodont Neanderthals uniting with a cynodont people to produce a mixed offspring, or taurodont pre-Neanderthals (? Heidelberg) uniting with a cynodont people to produce mixed Neanderthals.

However that may be, it is evident that the condition of taurodontism has occurred over an immense period of time and is not, so far as the present records show, absolutely distinctive of one particular race only. It is possible that the teeth of fossil apes (the Taubach molar) exhibited the condition. Eoanthropus also may possibly provide an example of the character and there is no doubt that the teeth of Heidelberg man and of many of the Neanderthals exhibited the condition of taurodontism to a marked degree.

It has been stated that in modern races the pulp cavity is relatively larger in teeth of young persons than in the teeth of adults and that this relatively large pulp character as an infantile condition is the persistence of a character that is primitive for the Hominidae.

So far as the size of the pulp cavity is concerned, there is little doubt that teeth at an early age, not only in man but also in primates generally, do exhibit the condition of taurodontism to a more marked degree than do the teeth of adults.

It appears possible therefore that this infantile character does signify the

persistence of a primitive feature. In any case, as has been stated formerly, the condition of taurodontism is known to occur even in the teeth of *adult* modern individuals. The condition has been stated to occur in modern Europeans (Adloff figured a taurodont molar in a modern European, 1910, Plate X, Jaw *H*), in Mongolians (the Eskimo, according to Kramberger) and is definitely present in South African races, including Australoid peoples.

From the occurrence of taurodontism, and the association of very primitive characters with taurodontism, in apes from early Pleistocene times, in primitive human fossil races from the earliest chapters of our history, in the developing teeth of primates generally and in the teeth of adults of many modern races, it appears that there is considerable support for the view that taurodontism is a primitive character.

If taurodontism is a primitive character it is evident that all taurodont races have sprung from one stock and that all cynodont races are offshoots from this taurodont type.

Whether taurodontism is a primitive feature or not, we must believe that either all taurodont races have sprung from one stock or that there has been convergent evolution at different geological stages in human history.

Although many authorities consider that the taurodont Neanderthal race represents a side branch of the human race which became wholly extinct in western Europe, other authorities (e.g. Hrdlička, 1914) state that Neanderthal characters are met with in individuals in Europe in periods later than the Palaeolithic and even in present-day populations, and that such characters should be regarded as atavisms showing reversion to that ancient race. That is to say, it has been stated that traces of Neanderthal blood and physiognomy are not lacking even in modern Europeans and that such characters, and evidently the characters of taurodontism also, should be regarded as atavisms showing reversion to the Neanderthal race.

This is a question which obviously needs further investigation by scientists in Europe. We do not know what the fate of the Neanderthal race in Europe was, but it is possible that analysis of the incidence of taurodontism in Europeans may yet reveal that fate. In other regions, e.g. Africa, it is possible that this race or some closely allied taurodont group has survived into a later epoch and is responsible for the character of taurodontism here.

The discovery of the condition in living South African races and in other races widely separated geographically certainly indicates, in the writer's estimation, that we may have to admit that these characters, thus placed in parallel, are not convergent but derivative. Until convergence can be demonstrated it certainly seems preferable that the character of taurodontism be regarded as primitive and the people possessing taurodontism as having come from one stock. In other words, dental comparisons indicate a familial relationship between Heidelberg man, Neanderthal man, Boskop man and the South African Australoids.

## Concluding Remarks

This investigation has shown that a number of teeth discovered at Zitzikama exhibited the condition of taurodontism and that taurodontism is also of frequent occurrence in the teeth of living South African races. In none of the dentitions examined, however, was the condition of taurodontism as well marked as in the teeth of the Krapina or Jersey Neanderthaloids, even although in many instances the teeth examined exhibited the character relatively as clearly as the teeth of the Heidelberg jaw.

It was found that although the Bantu and Bush peoples possessed teeth of the cynodont type, taurodont teeth occur in South African hybrids where the elements of fusion are Australoid or Boskopoid with cynodont types. From this it was concluded that taurodontism is a character of South African Australoid and Boskopoid peoples.

The fact that taurodont races have intermingled with cynodont races of mankind and produced fertile offspring is considered to show that taurodontism is not a character of zoological species rank. The frequency of occurrence of the condition in hybrids showed that taurodontism is probably a Mendelian recessive character and since, in the Mendelian sense, taurodontism was found to breed true, it was concluded that taurodontism must be a character of at least variety rank.

Finally, from a consideration of these facts and from the frequency of occurrence of the character and its wide geographical and historical distribution, it was concluded that until convergence was demonstrated it appeared preferable to regard taurodontism as a primitive character and the people possessing the character as having come from one stock.

In conclusion, I desire to thank Prof. Raymond A. Dart for numerous helpful suggestions and criticisms during the investigation. I also wish to acknowledge my indebtedness to Messrs Krynauw and Le Helloco, students of this University, and to my friend, Mr W. Tamson, for the drawings with which this paper is illustrated.

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## EXPLANATION OF PLATE I

*Row A.* The Strandlooper molars (reading from left to right). Lower second molar, upper second molar, upper first molar, upper second molar, upper first molar, lower first molar. (From Zitzikama.)

*Row B.* The Boskop molars (reading from left to right). Lower second molar, lower first molar, upper second molar, upper first molar. (From Zitzikama.)

*Row C.* Bantu-Boskop hybrid's teeth (reading from left to right). Lower first molar, lower second molar, lower third molar, lower first premolar—all from the left side of one individual. (Skull 117.)

*Row D.* The Strandlooper anterior teeth (reading from left to right). Upper premolar, lower first premolar, upper premolar, upper canine, upper first incisor, upper second incisor. (From Zitzikama.)

*Row E.* The Strandlooper molar crowns (reading from left to right). Lower molar crown, lower molar crown, upper molar crown, upper third molar crown, lower molar crown, upper molar crown. (From Zitzikama.)

A
B
C
D
E

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# DIFFERENCE IN THE OSSIFICATION OF THE MALE AND FEMALE SKELETON

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Shortly after the announcement of the discovery of X-rays in 1895, I thought I saw an opportunity of using this method in a research, corroborating or correcting the time element in commencing ossification as given in the standard works of anatomy. It was not, however, until 1905 that I had collected sufficient data on which to base an opinion. I then published a brief account of my findings. This method seemed to me to be the only one in which a large number of subjects could be obtained, and the average time at which the centres of ossification were making their appearance determined with accuracy. In using living material for this examination a subject of desired age could be selected and could be subsequently re-examined for months, or even years as the results indicated. The rate of growth could thus be determined while in other subjects the times of appearance of centres of ossification could be estimated with reasonable accuracy. I understood that the older method of microscopic observations with serial sections would necessarily be very limited. The specimens had to be obtained from the dead house, and the labour involved would preclude the examination of large numbers and the data could not be as accurate as those obtained from the living subject.

In 1906, the date of my second publication, I felt justified in announcing the following conclusions:

*First.* The process of ossification is inaugurated much sooner than has hitherto been supposed.

*Second.* The bones of the female ossify in advance of those of the male. This advance may be measured in early stages by days, later by months, and subsequently by years.

*Third.* The chronological order of ossification of the bones of the carpus is different from that formerly supposed.

*Fourth.* The bones of a first child ossify, as a rule, sooner than those of subsequent children.

*Fifth.* Ossification is bilaterally symmetrical regardless of variations (normal) which may occur.

*Sixth.* The union of the epiphyses with the diaphyses takes place much sooner than was formerly supposed.

*Seventh.* Variation in the ossification of bones is a heritable trait. The

difference in ossification of the male and female skeleton may be grouped as follows:

*First*, a comparison of the time of appearance of centres of ossification.

*Second*, the time of the union of the epiphyses with the diaphyses.

*Third*, there may be differences in chronological order of ossification.

In regard to the first two groups I can give abundant proof.

I have given very little attention to the third group and will refer to it in brief only.

My conclusions are based upon the study of nine hundred and ninety-four Roentgenograms of which one hundred and forty are foetuses between the ages of ten and a half weeks and thirty-eight weeks; one hundred new-born babes between the ages of one hour and seven days; five hundred and fifty-four children between the age of three months and twelve years and two hundred from twelve years to twenty-three years of age. From an examination of the five hundred and fifty-four hands of children, noting the size of the centres of ossification in mm. of the bones of the carpus, there was abundant evidence that the bones of the female are much in advance of those of the male and I estimated the time of appearance of these centres as follows:

CARPUS

1. *Capitatum.*
   Female: between the third and sixth month.
   Male: between the fourth and tenth month.
2. *Hamatum.*
   Female: between the fifth and tenth month.
   Male: between the sixth and twelfth month.
3. *Triquetrum.*
   Female: between the second and third year.
   Male: about three years of age.
4. *Lunatum.*
   Female: between the third and fourth year.
   Male: about four years of age.
5. *Navicular.*
   Female: at four years of age or early in fifth year.
   Male: about five years of age.
6. Lesser *Multangular.*
   Female: between the fourth and fifth year (preceding the greater multangular).
   Male: between the fifth and sixth year (preceding the greater multangular).
7. Greater *Multangular.*
   Female: between the fourth and fifth year (preceded by the lesser multangular).
   Male: between the fifth and sixth year (preceded by the lesser multangular).

8. *Pisiform.*
   Female: between the ninth and tenth year.
   Male: between the twelfth and thirteenth year.

A table giving the name, sex, age, and size in mm. of these centres has been published, and I will only explain and describe a few, sufficient, however, to demonstrate the differences between the two sexes. Fig. 1 illustrates a case in which ossification is much in advance of the average. In this hand of a girl, age one year, two months and twenty days, it was known that ossification of the capitatum and hamatum had commenced several weeks before birth and

Fig. 1.

Fig. 2.

Fig. 1. Female, age one year, two months, twenty days. The capitatum and hamatum began to ossify several weeks before birth, and the triquetrum when about eight months of age.
A number of the epiphyses had commenced ossification before the close of the first year, some of them as early as the eighth month. The epiphysis of the radius at birth or shortly after birth (reduced $\frac{2}{3}$).

Fig. 2. Female, age one year and nine months. The capitatum and hamatum began to ossify before birth. The epiphysis of the radius soon after birth and many of the epiphyses of the metacarpal bones and the phalanges before the close of the first year (reduced $\frac{1}{2}$).

that of the triquetrum when about eight months of age. A number of the epiphyses had commenced to ossify before the close of the first year, some of these as early as the eighth month. The epiphysis of the radius must have been present at birth. While this hand is in advance of the average, it is not a rare exception, as is shown by fig. 2 which represents the hand of a girl of twenty-one months and shows a condition of ossification much in advance of any male of corresponding age that I have seen. I could quote a large

number of similar cases, but space will not permit. Figs. 3 *A* and 3 *B* illustrate the hand of a male of eight months of age and that of a female eight months old respectively. In the male hand there is a small centre of ossification in the hamatum while in the female there are large centres in the capitatum and hamatum. In the female ossification in the two bones began before birth; in the capitatum about the thirty-eighth week of intra-uterine life. Fig. 4 illustrates the hand of a female five years of age. This is an example of the erratic course sometimes found in the chronological order of ossification of the bones of the carpus. It is to be noted that the lesser multangular is in the fourth position in order of ossification. I have found it in this position nine times out of one hundred and six cases. It is also to be noted that the greater multangular occupies the fifth position. I have found this bone occupying the fourth position in seven only out of one hundred and six cases. The navicular is in the sixth position and the lunatum in the seventh. I have found the lunatum occupying this position in six out of one hundred and eighty-six instances, and they were all females. I would suggest that this fact may be of some significance.

The usual chronological order is as follows: (1) the capitatum, (2) the hamatum, (3) the triquetrum, (4) the lunatum, (5) the navicular, (6) the lesser multangular, (7) the greater multangular and (8) the pisiform. In two hundred and twenty-nine subjects the capitatum occupied the first position in two hundred and twenty-five cases, and the second position in four cases only. The hamatum was four times in the first position and two hundred and twenty-five times in the second. The triquetrum is in the third position in which it was found in two hundred and eleven cases, and in the fourth position in ten cases. It is never displaced from this, its normal position, by other bones except by the lunatum. The position of the lunatum is fourth and it was thus found in one hundred and fifty-eight out of one hundred and eighty-six cases. The navicular occupies the fifth position in which it was found in sixty-eight out of one hundred and eleven cases. The lesser multangular occupies the sixth position in which it was found forty-seven times in one hundred and six instances. The position of the greater multangular is seventh, a position in which it was found in forty out of one hundred and six instances. The pisiform is the last bone to ossify and consequently occupies the eighth position. I have explained this at some length for the reason that the correct order of ossification has not yet found its way into textbooks of anatomy. The difference of ossification in male and female was shown in a very spectacular way by the examination of twins of the same sex (female) and of twins of opposite sex. In the former the ossification of the carpus of the two girls seven years of age was identical. In the latter, a boy and a girl five years of age, the difference in ossification is very pronounced. In the girl's hand three bones, viz. the navicular, the greater and the lesser multangular, had all very definite nodules of ossification while the three corresponding bones in the boy's carpus showed no indication of ossification whatever. The limits of this

Fig. 3 *A*.

Fig. 3 *B*.

Fig. 3 *A*. Male, age eight months. The hamatum shows a small centre of ossification.
Fig. 3 *B*. Female, age eight months. The capitatum and hamatum began ossification before birth.

Fig. 4. Female, age five years, one month. The chronological order of ossification of the carpus is unusual and is as follows: the capitatum, hamatum, triquetrum, lesser multangular, greater multangular, navicular and lunatum, which last bone is in the seventh position, its usual position being fourth.

paper will not permit me to dwell upon the union of the epiphyses with the diaphyses. In my last paper published in the *American Journal of Physical Anthropology*, I gave the results of the examination of sixty-four male and eighty-one female hands. In the female hand complete union of the epiphyses of the metacarpal bones and of the phalanges was found at sixteen years of age. I have found them united at fourteen years and three months in the female hand (fig. 5), while the earliest case in which these epiphyses were united in the male hand was in one of the age of seventeen years and four months. In some instances I have found them united in the male hand between eighteen and nineteen, but in most cases it is not completed in male hands until between

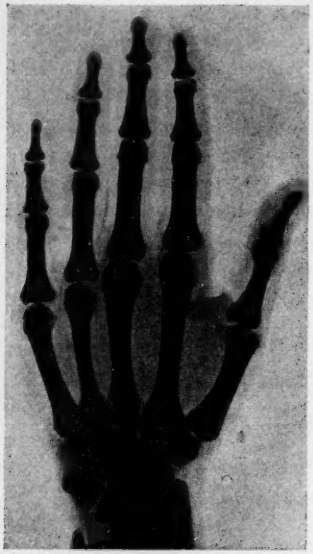

Fig. 5. Female, age fourteen years, three months. All of the epiphyses of the metacarpal bones and the phalanges have united with the shafts.

nineteen and twenty years of age. It will thus be seen there is a difference of three years between the two sexes. I think this is an anatomical fact of surgical importance and should be known and recognised. I have reserved consideration of embryos and of the new-born babe for the latter part of this paper.

I have not been able to study a sufficient number of cleared embryos to make positive statements as to the appearance of the earliest centres of ossification.

Unfortunately with the cleared embryos I have examined, the sex was not noted before the clearing process, and as regards older embryos in which the external genitalia could be distinguished, I have examined a few specimens

only. In a fifty-two mm. female embryo, age ten and a half weeks (fig. 6, 1), a large centre of ossification in the ilium and a small centre in the ischium are apparent. This condition is to be compared with that of a sixty-two mm.

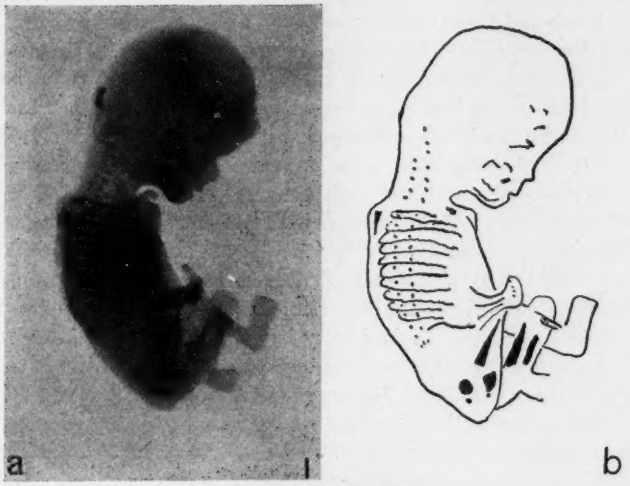


Fig. 6, 1. Embryo 52 mm. female.

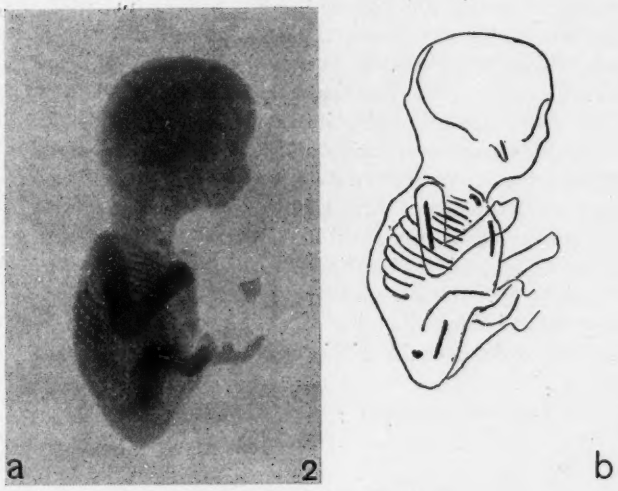


Fig. 6, 2. Embryo 62 mm. male.

male embryo, age eleven weeks (fig. 6, 2), in which there is a very small centre in the ilium and none in the ischium. In the female there are a large number of centres in the vertebrae while very few if any are to be seen in the male

embryo. In the study of one hundred new-born babes there is abundant proof of the difference between the two sexes. The parts observed were the carpus, the tarsus, the epiphyses at the distal extremity of the femur and at the proximal extremity of the tibia. In the paper published on this subject the size in mm. of these centres was given and comparisons made.

I will discuss two of these, the most advanced female and the most advanced male. In the male hand a minute centre of ossification in the capitatum and medium-sized centres in the epiphyses of the femur and of the tibia and somewhat larger centres in the calcaneus and talus were present. In the female hand centres of ossification were present in the capitatum and hamatum several weeks before birth and the epiphyses of the femur and tibia were quite large. Large centres of ossification were present in the calcaneus and talus and all of these were at least double the size of those seen in the male. A large centre, not present in the male, was to be seen in the cuboid. I have been asked a number of times if it would be possible by this method to determine the sex of the foetus *in utero*. Undoubtedly it would be possible in some instances provided one could produce a Roentgenogram showing what is to be seen in an isolated embryo. Had a Roentgenogram been made at the thirty-second week of intra-uterine life all of the centres mentioned above except those of the carpus might have been present and had this been the case one could have said positively that it was a female. However, in my experience, it is impossible to make these Roentgenograms. I have made a number of Roentgenograms of the foetus *in utero* in which the entire skeleton could be well seen, especially the skull, the vertebral column, the ribs and all the long bones, but the epiphyses could not be seen. Even if it were possible to make these Roentgenograms I do not see any practical value in the determination of sex before birth; but from a medico-legal point of view the determination of sex after birth by means of an examination of the bones of the skeleton is of the greatest importance. With the data I have at hand groupings of these could be made, or the absence of these centres shown, by means of which the sex, in a large percentage of cases, could be identified. Of course slow ossification in both sexes and rapid ossification in both sexes making exceptions to the rule are met with. With a more comprehensive study of the subject and additional data, I think groupings could be made whereby identification of the sex of the skeleton could, within reasonable limits, be made possible.

# AN ISCHIOPAGUS

By JAMES OAG, M.A., M.B., Ch.B. (Edin.)
AND
S. W. DRINKWATER, M.B., Ch.B. (Vict.), F.R.C.S. (Eng.)

The occurrence of any strange and unexpected condition in the course of one's work as a general practitioner provides a refreshing and stimulating relief from the mass of everyday ailments and disorders. Recently it was the fortune of one of us to encounter a most unusual type of monstrosity in the course of a midwifery case—an exceedingly well-developed example of an ischiopagus.

## CLINICAL FEATURES

Mrs B., aet. 47, multipara, was attended by a midwife at her last confinement. After a few strong pains the membranes ruptured, and a child's head and shoulders were rapidly born. In spite of strong and continuous pains, no further progress occurred in the labour. After waiting two hours the midwife sent a request for medical assistance.

Examination of the patient at this stage showed a partly-born child presenting at the vulva, its thorax apparently firmly gripped by a tightly contracted uterus, whilst there was still a large mass to be felt in the abdomen. The patient was only slightly exhausted.

The os was dilated manually and, with surprisingly little difficulty, a hand was introduced, which, passing up the back of the trunk, encountered and brought down two lower limbs. It was felt that the trunk continued upwards, and then two more lower limbs were met. When these had been grasped and folded on to the ventral surface of the foetus, a monster of most striking appearance, with two joined trunks, two full-sized heads, and a pair of legs projecting laterally on each side, was delivered easily. Encircling the thorax of the first-born trunk was a deep bruise, where the contracting uterus had held it firmly. Within ten minutes a very large single placenta with one central cord came away.

The patient made an uneventful recovery. All her previous labours had been uneventful, and all her children healthy.

## EXAMINATION OF MONSTER

### External Features

The appearance is that of two well-developed, apparently full-term foetuses, one somewhat larger than the other, united at the lower end of the trunk. The lower part of the abdominal wall is continuous from one foetus across the

line of union to the other, with a single umbilical cord in the centre of this line. At each side of the line of union is a pair of legs. Between the legs, on one side are normal female external genitals and anus, on the other side a single orifice only, and a small tubercle ventral to this. The head, thorax, arms and upper abdomen of each foetus are normal in appearance (fig. 1).

### Internal Features

On dissection, the abnormalities seen are almost confined to the lower abdominal and pelvic regions, and, if the kidneys be excepted, are of two

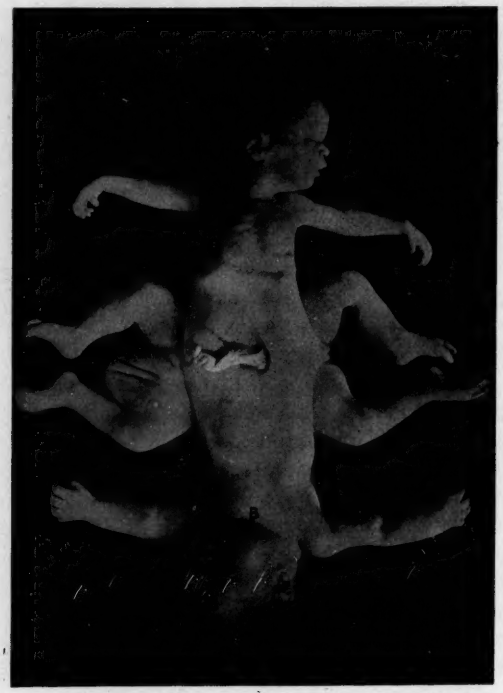

Fig. 1. Ischiopagus.

kinds: first, in the alimentary canals, a part is common to both foetuses, and secondly, bilateral structures which normally are connected to each other, join the corresponding part of the other foetus.

*Skeletal and Muscular Systems.* Above the lumbo-sacral junction, the two skeletons show no deviation from the normal. The innominate bones of each foetus, instead of joining ventrally, are splayed out and joined with those of the other foetus, the right of one with the left of the other, so that two laterally

placed pelvic cavities are formed, with a symphysis pubis between the legs on each side. The two sacra curve laterally into one pelvis, the deeper of the two, and as they lie closely side by side, the adjacent lateral parts of the third, fourth and fifth pieces, are joined by cartilage. By the junction of the third pieces the other pelvis is closed behind.

The muscular and ligamentous structures in the floor of the more complete pelvis present no gross abnormality. In the other pelvis, absence of the sacrum is compensated by a strong fibrous raphe, extending forwards from the above-mentioned point of union of the sacra, and giving origin to the two pyriformis and gluteus maximus muscles. The gluteal muscles take origin also from the back of the corresponding sacra. A dense fibrous sheet separates the pyriformes from the glutei. No sign of the levatores ani or sacro-sciatic ligaments is to be seen. There is evidently an attempt to produce a normal pelvic floor in the absence of the sacrum from this side.

*Digestive System.* The two alimentary canals are normal as far as the commencement of the jejunum, except that the great omentum of one (*B*) passes to the posterior abdominal wall instead of to the colon. Liver, gall-bladder, spleen and pancreas of each foetus are normally situated and have the usual peritoneal relationships. A patent umbilical vein passes from the cord to each liver. The larger foetus (*B*) has a liver (237 gm.) four times the size of the other (*A*—60 gm.). In each foetus the small intestine lies closely coiled under the right lobe of the liver; from here the two terminal parts descend almost vertically and meet in a T-shaped junction. The vertical limb of the T, consisting of the terminal four or five inches of ileum, caecum with two vermiform appendices, and twelve inches of colon, is common to both canals (fig. 2). The colon proceeds transversely across the abdomen along the line of union of the bodies, and finally bifurcates. One limb passes into each pelvis, where it occupies the usual position of the rectum. In each foetus, one continuous mesentery, fixed only along the anterior border of the pancreas, passes to the whole small intestine and to one side of the common gut, and carries the superior mesenteric vessels (fig. 2). The common bowel has therefore two mesenteries. At the point of bifurcation of the common bowel, the superior give place to the inferior mesenteric vessels. These conditions suggest union, or rather failure of division in the distal limb of the U-loop of the mid-gut, with consequent non-rotation of the loops.

*Urino-genital Systems.* Within the more complete pelvis the viscera are normal and patent. The origin of the ovarian artery on each side from the aorta of the foetus of that side, and the presence of a well-marked ridge in the posterior vaginal wall, indicate the double origin of the internal genitals. Within the other pelvis, the rectum opens by a narrow channel into the neck of the bladder, posteriorly. From the bladder a narrow passage, an inch long, leads beneath the pubic arch into a large subcutaneous sac, occupying the whole of the inner side of the left thigh. This sac, which contains meconium and fluid, opens on the surface by the single orifice mentioned earlier. Its lining is

stratified squamous epithelium, that of the passage leading to it is columnar. The condition is evidently a persistence of a primitive form of cloaca. In this pelvis the two Mullerian ducts, one from each foetus, have remained separate. Two single-horned uteri, each with a distinct vagina, lie in apposition between the bladder and rectum. The vaginae are blind below, but two fibrous cords on the dorsal aspect of the cloacal passage suggest their continuation.

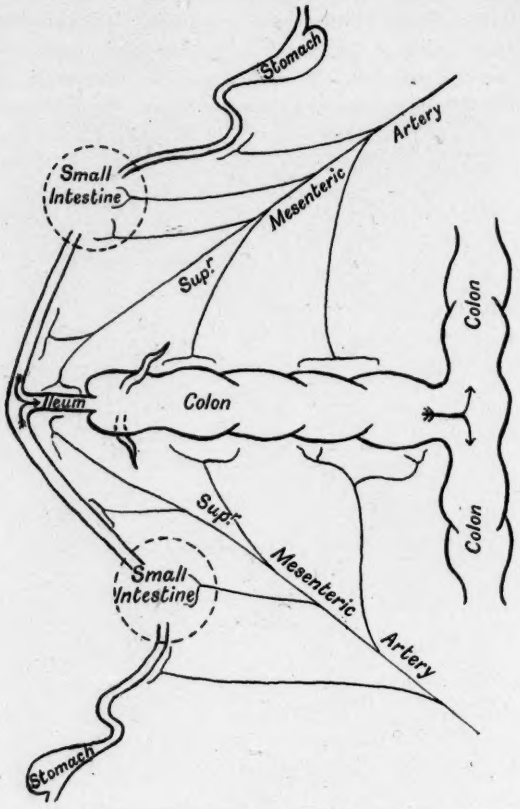


Fig. 2. Alimentary canal (diagrammatic).

A single kidney of irregular shape lies to the left of the vertebral column of each foetus, at the level of the pelvic brim. In one case (*B*) it connects with both bladders by two ureters emerging at separate hila. In the other (*A*) could be found only the left ureter, leading to the bladder in the less abnormal pelvis. The latter kidney (12 gm.) is exactly one-half the size of the former. Both suprarenal glands of each foetus occupy the usual position against the crura of the diaphragm. The left glands have the appearance of a solid, coiled tube.

*Other Systems.* Two umbilical arteries only are present in the cord, and both come from the more complete pelvis; one is therefore derived from the internal iliac artery of each foetus. The two vascular systems follow the plan of the skeletons and call for no further comment. The nervous systems follow the same arrangement and are therefore quite separate throughout their extent. All the limb plexuses are normal, and on tracing the lumbo-sacral plexus it is seen that the two legs nearest to a head belong to one foetus. Ossification has commenced in the lower ends of the femora and upper ends of the tibiae of all four legs.

Above the level of the diaphragm, the structures are normal in each case, and retain the foetal characters, since breathing never occurred.

## COMMENTS

Of the symmetrical double monsters, ischiopagi are a rare type. This specimen is remarkable for the high degree of perfection attained. The dissection shows that one part only of the twin foetus has failed to be duplicated —the distal limb of the mid-gut. Cases described by others have shown an almost identical condition of the bowel, which must therefore be the factor determining the particular form of the monster.

A perusal of the literature of symmetrical double monsters shows that, craniopagi excepted, they have certain constant features. First, the central nervous systems are always separate and distinct. Secondly, the digestive tube in some part of its course is single; this part always includes a portion of the mid-gut, and may or may not extend a variable distance into the fore- and hind-gut. Thirdly, the mesodermal structures, such as the vertebral columns, accommodate themselves to the altered conditions of other parts, and show evidence of at least an attempt at doubling, which may be masked by crowding together of adjacent structures.

The formation of these double monsters is evidently related to a partial failure of the archenteron to follow division of the remainder of the embryo, and the form taken by the resulting monstrosity is determined by the extent of this failure.

We are indebted to Prof. J. S. B. Stopford, in whose department the dissection was carried out, for the facilities afforded us.

# NOTE ON A CASE OF ANOMALOUS RIGHT VERTEBRAL AND SUBCLAVIAN ARTERIES[1]

By W. F. WINDLE, F. R. ZEISS and M. S. ADAMSKI
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In the course of dissection of an old male negro subject (approximately sixty years of age), an interesting group of arterial anomalies was observed. The first branch from the arch of the aorta was a short common trunk, about one and one-half centimetres long, for the two common carotid arteries. The second branch was a normal left subclavian artery. Posterior, inferior and slightly to the left of this arose the third and last branch, the right subclavian artery.

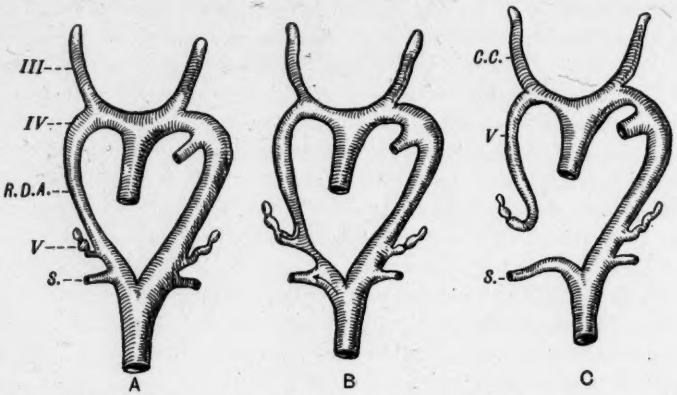


Fig. 1. To illustrate the generally accepted theory of the formation of an anomalous right subclavian artery with the vertebral as a branch of the right common carotid. III = third arch; IV = fourth arch; *R.D.A.* = right dorsal aorta; *C.C.* = common carotid; *V.* = vertebral; *S.* = subclavian. (After Cairney.)

This passed horizontally and to the right, posterior to the trachea and esophagus and anterior to the thoracic duct, which was normal, and the body of the third thoracic vertebra. Then, after turning superiorly and arching over the apex of the lung, it assumed the normal relations. The branches of the left subclavian were normal, but the right one possessed no vertebral branch. Instead, this artery arose from the right common carotid, and, after a course of about five centimetres, it entered the foramen transversarium of the fifth cervical vertebra. The right recurrent nerve hooked under the right inferior thyroid artery and passed medially and slightly superiorly behind the vertebral and common carotid arteries on that side.

[1] Contribution number 126.

Although cases of right subclavian arteries arising from the aortic arch are not uncommon[1], this anomaly associated with the high vertebral branch of the common carotid has not often been reported (about eighteen cases). In very comprehensive studies of aortic arch anomalies, Poynter[2] and Cairney[3]

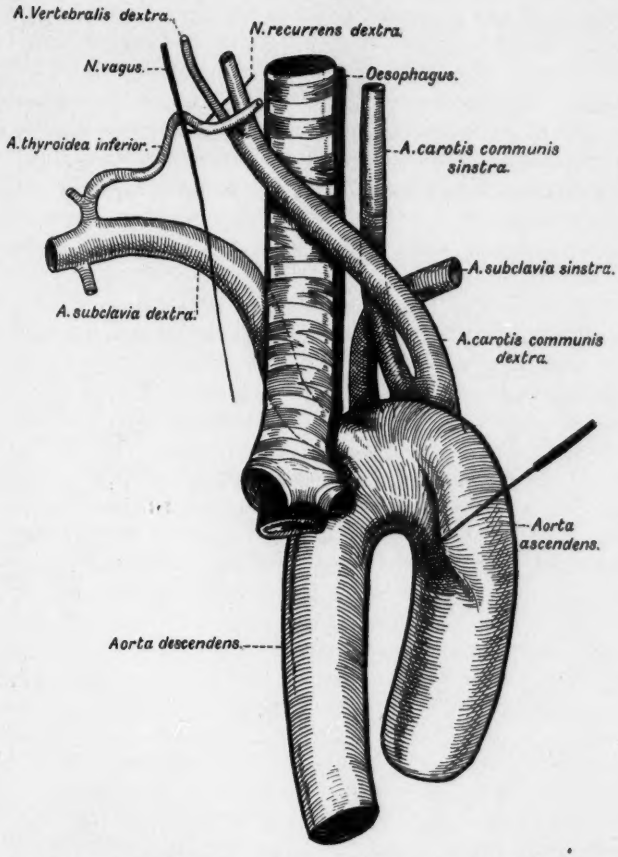


Fig. 2. A semi-diagrammatic illustration of a dissection showing the origin and course of the anomalous right subclavian and vertebral arteries. The ascending aorta and aortic arch have been pulled toward the left.

[1] An unreported case of right subclavian arising as the last branch of the aortic arch was observed last year in the Harvard Medical School laboratory by Doctor B. J. Anson.

[2] Poynter, C. W. M., 1916. "Arterial anomalies pertaining to the aortic arches and the branches arising from them." *University Studies, Lincoln, Nebraska*, vol. XVI, pp. 229–345.

[3] Cairney, J., 1925. "The anomalous right subclavian artery considered in the light of recent findings in arterial development; with a note on two cases of an unusual relation of the innominate artery to the trachea." *Journ. Anat.* vol. LIX, pp. 265–296.

have reviewed the significance of this quite adequately. It is enough to say that the right fourth aortic arch, instead of pinching off at its junction with the left one (dorsal aorta), probably has divided just distal to the vertebral branch. This has left the ventral segment incorporated in the vertebral and the dorsal segment in the subclavian. Such a separation may be due to an origin of the vertebral from a segmental vessel higher than the seventh. While the right recurrent nerve loops around the inferior thyroid artery, it also bears the same relation to the vertebral that it would normally bear to the subclavian; this, of course, is evidence that the proximal part of the vertebral artery represents part of the fourth right aortic arch. The fusion of the two common carotids is possibly due to the lack of a definite traction of the subclavian trunk upon the vessel that would normally be the innominate artery.

# REVIEWS

*Anatomie Comparée du Cerveau.* By R. ANTHONY. (Librairie Octave Doin, Paris.) 1928. Pp. 359. Price 70 francs, net.

This is a series of lessons on the brain by the distinguished professor at the Natural History Museum of Paris. They are lessons in truth, and are free from that divagation which is the sin of most modern neurologists. Anthony, like a Scotch dominie imparting the Euclidean method, treats us to an orderly procession of demonstrations in the grand manner of the Victorian morphologists. The chapters dealing with the telencephalon, the rhinencephalon, the neopallium and the corpus striatum afford that sureness of touch which comes of much devotion. He belongs to the group of splendid wooers of the brain as distinct from the prolific but tedious husbanders who think that the whole secret of life is wrapped up in the brain of Amblystoma. Here is a realist in neurology, free from the despondencies of book-learning; a lover of old ways in comparative anatomy who refuses to believe that the methods of his glorious predecessors can turn into nought that avails.

The shape, externally and internally, of the telencephalon is discussed with the aid of casts of the cerebrum and of the ventricles. The consideration of the changes in shape with increase in volume, of the changes in the flexures and in the shape of the cavities, is a testimonial to the value of that study of casts which has attracted so many of our abler anatomists. On this point of the lessons to be derived from casts, it is a pity that the author has not given us more from his valuable store. The treatment of the rhinencephalon is excellent and the survey of the macrosomatic and microsomatic brains in relation to that of the Primates is the most concise and clear of any recent publications. The neopallium is admirably demonstrated and the ontogenetic and phylogenetic character of the fissures is handled in such a manner as to dispel many difficulties. The problem of decussation is kept much to the fore and the olfactory decussation is depicted in a series of diagrams after the style of the familiar pictures of the optic chiasma. Recently the gustatory chiasma has been clearly described in the rat and we would like to see a brief account of the various chiasmae of the sensory side. Similarly one requires a much more definitive account of the relation of the anterior commissure to the other commissures on the one hand and to the rhinencephalon and neopallium on the other. The anterior commissure affords a series of problems, and an exact account of the termination of its fibres in the olfactory, temporal and occipital lobes in Man and in the Anthropoids may throw much light on the relative development of olfaction in these forms. A reference to the standard work of Kappers will show how difficult it is to obtain exact information on this point.

Such a book as Anthony has given us must have lacunae. In the first place, the introductory chapter is fraught with a certain nervousness and could be improved by the adoption of those classical diagrams of Gaskell so as to show that the sympathetic and parasympathetic system have to be relegated to the background but not forgotten. The conducting paths of the brain and cord might be described in more detail, so as to stress both the phylogeny and the clinical aspect of the syndromes which are gradually emerging, either in terms of the behaviourist or in terms of the clinical neurologist. The hypothalamus, the pons, the cerebellum, and the brain stem are worthy of more detailed treatment.

The portion of the book which deals with the size of the brain is peculiarly the work of Anthony in the rôle of Anthropologist as distinct from Comparative Anatomist. An unkind critic has said that Anthropology is the toy of the aged anatomist. A younger iconoclast has said that Anatomy is the study of dead men by live men, whereas Anthropology is the study of live men by dead. To one who has read Shaw Bolton, Donaldson and Havelock Ellis, this section of the book has certain attractions. There are valuable tables of brain-weights in relation to body-weights for classes, species and genera. The various attempts by Brandt, Bischoff, Snell and Manouvrier to find an index of brain-body-weight are reviewed. The independent efforts of Dubois to establish a coefficient of cephalisation are described. Dubois and Manouvrier see the brain in terms of body-weight and liver-weight respectively. The morbid anatomist would object to either denominator, for body-weight and liver-weight are so variable in fat content. But this is a quibble.

Anthony has instituted an Index of Cerebral Value which is an expression of the ratio of the brain-weight at a particular age to that of an adult which has been reduced to the somatic proportions of this particular age. The index ranges from 0·51 at birth to 1·21 at seven years of age in Man; it reaches a value of 1·0 at 45 and then decreases slowly to 0·93 in old age. These indices serve to give an idea of the relative rate of growth of the brain in relation to body-weight during the various age periods. It appears from his results that the Orang brain reaches its definitive weight at six months, the Gorilla and the Chimpanzee at two to three years. It is interesting to note that the weight of the Cat's brain at birth is about one-fifth of the weight at the sixth month, whereas the Bear at birth has a brain-weight of one-sixtieth of the adult weight.

As regards preservation of the brain. Anthony advises immersion in saturated salt solution to which is added from 3 to 10 per cent. of formol according to the size of the brain. A small piece of copper foil is added to stain the gray matter. Some of the other methods of staining the brain grossly, such as that of Ganz (*Brain*, 1923, vol. XLVI, p. 128), might well be included for the benefit of the myopic neurologists of the younger generation.

*Atlas der Histotopographie gesunder und erkrankter Organe.* By Dr ERWIN CHRISTELLER. Berlin. (Thieme; Berlin.) 1927. 88 tables and 182 three-colour photograms. Price 90 marks.

In this beautiful example of German bookmaking the Director of Morbid Anatomy in the Rudolph-Virchow Hospital, Berlin, attempts to portray the pathological lesions of the body by actual colour photographs of whole organs. He has undertaken a task which has long awaited some pioneer in the teaching of microscopic anatomy. It is not possible to expect the student to learn much from an examination of a small piece of tissue under the microscope. Every teacher knows how difficult it is to persuade the student to make a drawing of each section. It would be far better to provide the student with large sections through a whole organ, such as the breast, heart or bladder and urethra, and allow him to spend a whole session of the class in the examination of the gross and microscopic anatomy thereof. The effect upon the student of examining a longitudinal section of the kidney and suprarenal cannot be over-estimated, and the time spent in drawing such a section is a powerful aid to gross anatomy and topographical relations. About 30 plates illustrate whole sections of whole organs in health and there are several plates of anatomical deformities such as pyloric stenosis and of normal organs in pregnancy. One looks forward to a similar atlas of a wider range for the student of normal histology.

*The Chemical and Physiological Properties of the Internal Secretions.* By E. C. DODDS and F. DICKENS. (London: Humphrey Milford, Oxford University Press.) 1925. Pp. xii + 214. Price 8*s.* 6*d.* net.

The history of the endocrine system has much in common with that of the cinematograph. The terrain has been occupied in turn by the clinician, the physiologist and the bio-chemist, and now the pioneers run the risk of oblivion by reason of the prominence of the press agent, the caption writer and the producer who wishes to do Hamlet in modern garb. The historical account of the various internal secretions is one of the charms of the book and one notes but few omissions of any significance. It is hardly to be expected that Zuckerkandl and Balfour should fail to be forgotten along with Gaskell and others of the anatomical workers who did so much to arouse interest in the endocrine system.

The pancreas, pituitary, thyroid, ovaries, and suprarenals are described in turn and the history, chemistry and physiology are clearly pursued in a most lucid manner. On the one hand the chemical synthesis is presented so as to satisfy the chemist, and on the other the clinical application of the chemical product is reasonably assessed. Collip's recent work on the rôle of the parathyroid in relation to the calcium of the blood is included in the addendum to chap. VI. Harington's synthesis of thyroxin was announced too late for inclusion in the book. This book can be recommended to the anatomist and clinician no less than to the physiologist for it is a remarkable presentation of the triumphs of the British School of Physiology and Clinical Medicine.

*The Histology of the More Important Human Endocrine Organs at Various Ages.* By Dr E. R. A. Cooper. (London: Humphrey Milford, Oxford University Press.) 1925. Pp. xiii + 119, 61 figs. Price 12*s.* 6*d.* net.

This is a valuable effort at introducing some sequence into the minute anatomy of the endocrine glands in relation to their age changes. The pituitary, suprarenal, thyroid, parathyroid and thymus are dealt with in orderly fashion and the histological findings at the various ages are compared with the varying accounts of other observers. The book is of great use to the normal and morbid anatomist and the bibliography is of considerable length. In a future edition one would like to see a more extensive appreciation of the historical aspect, as, for instance, the part played by Zuckerkandl and Henle in the chromaffin system, and of the more recent quantitative work on the growth of the glands, such as the work of Scammon on the thymus. The microphotographs are particularly useful for purposes of comparison.

*Das Autonome Nervensystem.* By Erich Schilf, Berlin. (Thieme, Leipzig.) 1926. Pp. 207, 25 figs. Price 16.50 marks.

This is a sound review by an active member of the staff at the Berlin Institute of Physiology and confines itself essentially to the physiology of the sympathetic system from the commencement of the discoveries of Langley. The introductory section dealing with the sympathetic and parasympathetic from the anatomical point of view is brief and to the point. The innervation of the heart and blood vessels is followed by a résumé of the work on the innervation of the respiratory and uro-genital systems. The alimentary canal, the eye and the skin are adequately treated. The whole problem of glandular secretion is presented in a logical manner. The various attempts to elucidate the afferent side of the splanchnic system, on the basis of Head's clinical assumption that there is a protopathic afferent supply to the viscera, is an interesting indication of the trend of research, and the work of Boeke, Kulchitsky, Hunter and Royle in relation to the double innervation of striped muscle is accurately presented. The small amount of work in relation to the localisation of the centres for control of the vegetative system, along with the recent advances in the surgery of the system, concludes the review. The bibliography is not the least useful part of the work and an asset to the neurologist.

*Topographical Anatomy of the Dog.* By O. Charnock Bradley. (Oliver and Boyd, Edinburgh and London.) Second edition, 1927. Pp. 268, 80 figs. Price 24*s.* net.

Bradley's *Anatomy of the Dog* has served a three-fold purpose. It has been a standard textbook for the veterinary student, has been a substantial introduction to comparative anatomy for many medical students and has been a

laboratory companion to every physiologist. A number of new illustrations have been added by Murray and the book is considerably enhanced in value thereby. There is no difficulty in following the dissectional instructions and every effort has been made to satisfy the dangers of terminology. From the anatomical point of view it might be suggested that all cross-sections should be shown with the right side of the animal on the left hand of the observer, as this is the accepted convention of most biologists. In two ways the value of the book can be increased. In the first place a table of the root value of the nerve supply to the various limb muscles and a detailed diagram of the segmental value of the connections of the sympathetic system are one of the constant needs of the neurologist. On the other, details of the veins and their branches in the fashionable physiological regions are always in demand, especially as regards the submaxillary region, the portal system, the gall-bladder and the suprarenal. The frequency with which such operations as Eck's fistula and gastro-enterostomy are performed by the modern physiologist indicates the value of such an addition.

The section dealing with the brain and special sense organs is excellent and one can only wish for additional illustrations of the eye and ear, for even the external auditory meatus of the dog is a veritable labyrinth to the average anatomist.

*Methoden zur Untersuchung der Morphologie der Primaten.* By S. Oppenheim, A. Remane and W. Gieseler. (*Abderhalden's Handbuch der biologischen Arbeitsmethoden*, Abt. vii, Heft 3, Lief. 236; Urban and Schwarzenberg, Berlin.) 1927. Pp. 532–682, 69 figs. and 6 tables. Price 9 marks.

The first section of the book is devoted to Craniology and is essentially an exposition of the well known methods of Rudolph Martin and P. Hermann. The various indices are described and careful instructions are given. The space given to suture union is all too brief and one notes the omission of much of the work done by Bolk in Amsterdam and by Todd and Stevenson in America. The radiographic method of determining endocranial skull form, as described by Harris of London, might also have been included. The indices for the various skeletal bones are admirably collected together and such primitive characters as hair pattern and skin ridges are not neglected. Remane deals with the difficult problem of dentition and furnishes a very thorough series of measurements and indices for the individual teeth. Here again one feels that the anthropometrist has failed to make use of the information offered by the radiologist. Gieseler deals in particular with the long bones of the Anthropoids and includes certain measurements and indices referring to the epiphyses. This book contains little that is new to anyone acquainted with Martin's *Lehrbuch der Anthropologie*, and it is to be hoped that in the near future considerably more attention will be devoted to the radiographic method of examining the skull and long bones on the one hand and the teeth on the other.

*Atlas de Radiographie du Système Ossueux Normal.* By Drs HARET, DARIAUX and QUENU. Paris. (Masson et Cie, Paris.) 1927. Pp. 132, 123 figs. and 123 keys. Price 160 francs.

This atlas of normal radiography of the skeleton by two radiologists and a surgeon of the Paris Faculty is a decided improvement on most of its predecessors. They regard the radiogram as a permanent document and stress the need for accurate recording of the conditions under which it is taken. The position of the subject, the degree of flexion or extension of the joint, the centre of the ray relative to the field, the distance of the anticathode and the index of reduction of the radiograms are stated and all the radiograms of the limbs are right-sided. Alongside the radiogram in the text is an exact replica serving as a key, in which the outlines are traced distinctly and the salient anatomical points are labelled. This avoids the inconvenience of handling keys printed on transparent paper and allows both the radiogram and the key to be surveyed at the same time.

The adult skeleton is surveyed in order and is followed by a useful survey of the new-born child and infant. The radiogram of the pelvis of the new-born is not very clear as the centres for the costal elements of the ala of the sacrum are not clearly shown. In the radiograms of children of various ages it is interesting to see that the epiphysis of the os calcis is shown in the sixth year. This is correct notwithstanding a recent communication in the *Journal of Radiology* in which the appearance of this centre in the eighth year was regarded as abnormally precocious. The table of the dates of appearance of the primary and secondary centres of ossification which concludes the work is sound in this respect: it notes the wide range of time in the normal appearance of the centres. The radiograms of the pelvis might be done in greater detail and a time chart for eruption of the milk and permanent teeth would be of assistance.

This work is a serious attempt at establishing a regular course of teaching in Normal Radiography and indicates the folly of expecting the medical student to learn normal radiography in his chance acquaintance with the abnormal radiograms of the hospital service. Pour la connaître, il faut l'avoir apprise.

*Anatomischer Atlas (Toldt).* Revised and edited by Prof. HOCHSTETTER. Vienna; 13th edition. (Urban and Schwarzenberg, Berlin and Vienna.) 1927. Vols. I–III. Pp. 984, 648 figs. Price 36.60 marks.

The Anatomical Atlas of Toldt is as familiar a book in the hands of the anatomist and pathologist as any. The thirteenth edition has 32 new radiograms which are provided with transparent keys of unusual accuracy. This atlas needs no commendation. A teacher of Anatomy can do no greater kindness to the keen student than placing in his hand this book for reference during the course of his dissections so as to obtain at one and the same time a series of new views of the dissected parts and a familiarity with the German language.

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